

Impulsivity Affects Suboptimal Gambling-Like Choice by Pigeons

Jennifer R. Laude, Joshua S. Beckmann, Carter W. Daniels, and Thomas R. Zentall
University of Kentucky

Pigeons prefer a low-probability, high-payoff but suboptimal alternative over a reliable low-payoff optimal alternative (i.e., one that results in more food). This finding is analogous to suboptimal human monetary gambling because in both cases there appears to be an overemphasis of the occurrence of the winning event (a jackpot) and an underemphasis of losing events. In the present research we found that pigeons chose suboptimally to the degree that they were impulsive as indexed by the steeper slope of the hyperbolic delay-discounting function (i.e., the shorter the delay they would accept in a smaller-sooner/larger-later procedure). These correlational findings have implications for the mechanisms underlying suboptimal choice by humans (e.g., problem gamblers) and they suggest that high baseline levels of impulsivity can enhance acquisition of a gambling habit.

Keywords: gambling, suboptimal choice, temporal discounting, impulsivity, pigeons

Pathological and problem gambling among humans is clinically recognized as an impulse control disorder in which people show impaired behavioral inhibition and a failure to consider the long-term consequences of the decisions they make (*DSM-IV-TR*; APA, 2000). Suboptimal gambling behavior can be defined as repeated engagement in gambles in which the average net return is less than what is wagered (the proportion of positive to negative outcomes is less than 1.0). The decision to choose an alternative associated with a low-probability, high-payoff outcome (a jackpot) where losses occur with a greater frequency over an alternative that yields a high-probability low-payoff outcome (not gambling) over time involves a failure to maximize gains and minimize losses.

In humans, impulsivity has been defined as an enduring stable attribute that is part of a personality construct (as assessed by self-report measures; Bagby et al., 2007; Blaszczynski, Steel, & McConaghy, 1997). Impulsivity has also been defined by performance on delay discounting tasks (perhaps more appropriately called impatience when applied to delay discounting, see Green & Myerson, 2013) in which humans are asked about their preference for a smaller immediate reinforcer (typically hypothetical money is used) over a larger delayed reinforcer (e.g., Madden, Bickel, & Jacobs, 1999). In animals, actual food quantities have typically been used (Rachlin & Green, 1972). The steepness of the discounting function (the shorter the delay or larger the delayed reinforcer needs to be to compensate for the small immediate reinforcer) can be taken as a measure of the degree to which a subject is charac-

terized as impulsive, or conversely, the degree to which it lacks self-control (Hull, 1943). That is, behavioral measures of discounting are often interpreted as indicating degree of impulsivity by determining the rate of devaluation of a reward over time. Typically, multiple points on a choice/delay function are determined by either adjusting the delay or the amount of reinforcement until the subject is indifferent between small, immediate, and larger delayed rewards. These indifference points can then be plotted as a function of the delay to the larger reward as the magnitude of the larger reward increases (Madden & Johnson, 2010). Mazur's (1997) hyperbolic-decay model describes this function quite well.

Significant correlations exist between self-report measures of impulsivity and the rate at which delayed rewards are discounted by pathological gamblers (e.g., Blaszczynski et al., 1997; Petry, 2001; Vitaro, Arseneault, & Tremblay, 1997). It has also been found that the rate of delay discounting of monetary rewards for human gamblers is associated with impulsive choice and severity of problem gambling problem (Alessi & Petry, 2003; Dixon, Marley, & Jacobs, 2003; MacKillop, Anderson, Castelda, Mattson, & Donovan, 2006; Petry, 2001; Petry & Casarella, 1999). These findings identify an important component of impulsivity for human gamblers, a preference for a smaller-sooner over a larger-later reward.

The decision-making process observed in human gamblers has recently been modeled with pigeons (Zentall & Stagner, 2011). They found that pigeons reliably prefer an alternative that signals a low-probability, high-payoff outcome, even when this preference results in less overall reinforcement than an alternative that signals a high-probability, low-payoff outcome in which losses never occur. For the low-probability high-payoff alternative, a stimulus that always predicted 10 pellets of food was presented with a probability of .20, and a stimulus that always predicted the absence of food was presented with a probability of .80. The mean reinforcement per trial associated with this discriminative-stimulus alternative was two pellets. Choice of the other (high-probability, low-payoff) alternative produced one of two stimuli, both of which always predicted three pellets (see Figure 1). Importantly, all of the signals for reinforcement occurred immediately upon the choice response and when reinforcement occurred, it always occurred

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Jennifer R. Laude, Joshua S. Beckmann, Carter W. Daniels, and Thomas R. Zentall, Department of Psychology, University of Kentucky.

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Correspondence concerning this article should be addressed to Thomas R. Zentall, Department of Psychology, University of Kentucky, Lexington, KY 40506-0044. E-mail: Zentall@uky.edu

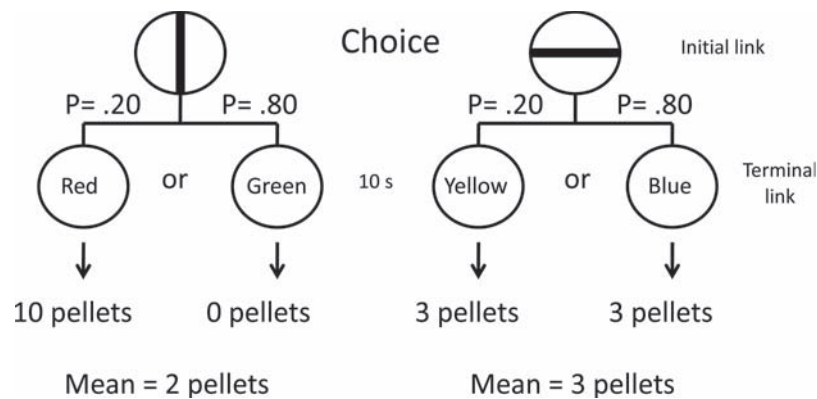


Figure 1. Experimental design of suboptimal choice training procedure. Pigeons were given a choice between two alternatives. Choice of one alternative produced either a stimulus (e.g., red) that on 20% of the trials was followed by 10 pellets of reinforcement or another stimulus (e.g., green) on the remaining 80% of the trials that was followed by zero pellets. Choice of the other alternative was followed by one of two stimuli (e.g., yellow or blue) each of which was followed by three pellets.

with the same delay following choice. Zentall and Stagner found that pigeons reliably preferred the suboptimal alternative that provided less overall reinforcement. This task would appear to be a reasonable analog of human gambling.

When Zentall and Stagner (2011) removed the discriminative-stimulus function from the gambling-like alternative by following each of the formerly discriminative stimuli (e.g., red and green in Figure 1) with both stimuli signaling a .20 probability of receiving 10 pellets, they found that the pigeons reversed their preference and reliably chose the alternative that provided a reliable three pellets over the alternative that provided a variable outcome that averaged two pellets. Thus, the pigeons were not just working to obtain the variability in outcome (sometimes 10 pellets, sometimes none) associated with the two-pellet alternative over the constant three pellets.

To determine whether the pigeon's task provides an appropriate analog of human gambling behavior, we used a comparable procedure to compare the choices of humans who reported gambling often with others who reported that they did not gamble (Molet et al., 2012). We found that humans who reported that they gambled chose the low-probability high-payoff outcome significantly more than control subjects.

Suboptimal choice by pigeons can be considered paradoxical because animals are arguably characterized as being optimal foragers (Stephens & Krebs, 1986). That is, they should be sensitive to the overall probability of reinforcement. However, when suboptimal choice has been found in animals, it has been explained by conditioned reinforcement theory (Fantino, Dunn, & Meck, 1979), which states that any stimulus that predicts reinforcement with a high probability will become a conditioned reinforcer and will elicit observing behavior (Dinsmoor, 1983). This account suggests that when an animal engages in suboptimal choice in this gambling-like procedure, the effective choice is between the stronger conditioned reinforcer associated with the discriminative stimulus alternative that signals 10 pellets and the weaker conditioned reinforcer associated with the optimal alternative that signals three pellets, rather than on the basis of the overall probabilities of reinforcement associated with the alternatives (two pellets vs. three pellets). What is not clear is why the stimulus associated with the

absence of reinforcement that occurs on 80% of the suboptimal-choice trials does not produce enough conditioned inhibition to offset the value of the infrequently occurring stimulus signaling 10 pellets, the stronger conditioned reinforcer.

Interestingly, certain conditions that are thought to increase attraction to the stronger conditioned reinforcer also have been found to increase choice of the gambling-like alternative. There is evidence that greater levels of food restriction are associated with greater rates of delay discounting by animals (Eisenberger, Masterson, & Lowman, 1982; but see Oliveira, Calvert, Green, & Myerson, 2013) such that hungry animals tend to show a greater preference for immediate rewards (Bradshaw & Szabadi, 1992; Snyderman, 1983), which seems highly functional in a natural setting. We have found that pigeons are less attracted to the gambling-like alternative when they are less food motivated and presumably less impulsive (Laude, Pattison, & Zentall, 2012). We proposed that the reduction in suboptimal choice observed in pigeons maintained on a less restricted diet was due to a decreased attraction to the stronger conditioned reinforcer. The idea that pigeons base their choice on the conditioned reinforcing value of the stimulus that predicts 10-pellets, rather than the overall probabilities of reinforcement, suggests that choice in this task may be a related to choices made in a delay-discounting task.

Parallel findings exist in the human literature showing a link between income and temporal discounting. For instance, lower income adults discount delayed rewards more steeply than do higher income adults (Green, Myerson, Lichtman, Rosen, & Fry, 1996). Furthermore, consistent with the proposal that there is a relation between suboptimal choice and impulsivity, it has been found that people from lower socioeconomic status tend to gamble proportionally more than those from higher socioeconomic status (Lyk-Jensen, 2010).

Another variable that has been shown to affect the degree of suboptimal choice in animals is social enrichment. We have found that pigeons given access to a large cage with conspecifics, compared with the more typical, smaller individual housing that allows for limited social interaction, showed reduced choice of the suboptimal alternative (Pattison, Laude, & Zentall, 2013). Interest-

ingly, research in the animal drug addiction literature has found rearing environment influences impulsive choice. For example, Perry, Stairs, and Bardo (2009) reported that socially enriched rats were less impulsive than isolated rats as measured by a delay discounting procedure. Thus, in our gambling task, it may be that spending time in a socially enriched environment (placed in a large cage with three other pigeons for approximately 4 hours daily) effectively reduced the attractiveness to the stronger conditioned reinforcer, consequently reducing choice of the suboptimal alternative.

The relation between the suboptimal choice task that has been used with pigeons (and humans) together with the fact that the rate of delay discounting of monetary rewards for human gamblers has been found to be a good predictor of impulsive choice and severity of gambling problem (Petry & Casarella, 1999) suggests that the same theoretical construct, impulsivity, may be involved in both tasks. Such a finding would provide additional support for the hypothesis that increased impulsivity might function to increase attractiveness of the stronger conditioned reinforcer resulting in an increased preference for the suboptimal choice.

It should be noted, however, that the suboptimal-choice and delay-discounting tasks differ methodologically in an important way. In the suboptimal-choice task, reinforcers occur at exactly the same time following choice; thus, there is no differential delay to reinforcement as there is with the delay-discounting task. In the suboptimal choice task, the delay to reinforcement associated with the two alternatives is exactly the same. For this reason, although several findings suggest that there is a relation between the two tasks, it would be informative to show that the two tasks are closely related.

One means of assessing delay discounting functions is with the use of an ascending-delay procedure developed by Evenden and Ryan (1996). With this procedure, pigeons, for example, are given a choice between one pellet of food immediately and four pellets of food over a series of 5-trial blocks with ascending delays. The first few trials in each block are forced trials in which the pigeon is exposed to the contingencies of reinforcement before the five choice trials are presented. With each successive block of trials, the delay increases. For example, Block 1 is associated with a 0-s delay, Block 2 with a 5-s delay, Block 3 with a 10-s delay, Block 4 with a 15-s delay, and Block 5 with a 20-s delay. This procedure is repeated for several sessions. Following stable performance, the percentage choice of the large reward is plotted as a function of delay to the large reward. In the present experiment, a version of this ascending-delay procedure was used to test the hypothesis that higher degrees of delay discounting are associated with increased suboptimal choice in our gambling-like task. In addition we manipulated the degree of social enrichment because social enrichment has been found to retard the development of suboptimal choice (Pattison et al., 2013).

Method

Subjects

Subjects were eight unsexed white Carneaux pigeons, 2 years of age, purchased from the Palmetto Pigeon Plant, Sumter, South Carolina. All pigeons were randomly assigned to one of two conditions: isolated or socially enriched. Pigeons in the isolated

condition were individually housed in wire cages measuring 28 cm wide, 38 cm deep, 30.5 cm high, in a colony room. The colony room was maintained on a 12h:12h/light:dark cycle. Pigeons in the enriched group were housed similarly to those in the isolated condition, but they were placed in a flight cage (see below for description) with three other pigeons for 5 hr per day, 5 days a week, for 90 days prior to the start of the experiment and following each experimental session. Throughout the experiment, all pigeons were maintained at 85% of their free feeding body weight and were given free access to grit and water. They were cared for in accordance with University of Kentucky animal care guidelines.

The flight cage measured 2.13 m high, 1.22 m wide, and 1.84 m deep and contained three shelf perches. The shelf perches were 31 cm, 61 cm, and 72 cm above the floor, respectively. All perches measured 32 cm long and 14 cm wide. Additionally, once every 5 days, a water basin half-full of water was placed inside the flight cage to give all the birds the opportunity to bathe.

Pigeons in the enriched condition were placed in the flight cage after they had completed their experimental session for the remainder of the day (between 4 and 6 hr).

Apparatus

The experiment took place in a Med Associates (St. Albans, VT) ENV-008 modular operant test chamber. The response panel in the chamber had a horizontal row of three response keys. Behind each key was a 12-stimulus inline projector (Industrial Electronics Engineering, Van Nuys, CA) that projected vertical and horizontal lines as well as the colors white, red, yellow, blue, and green. Reinforcement was delivered from a pellet dispenser that was mounted behind the response panel (Med Associates ENV-45). A 28 V, 0.1 A, houselight was centered above the response panel. A microcomputer in the adjacent room controlled the experiment. The same apparatus and subjects were used in both the delay-discounting task and the suboptimal choice procedure.

Delay Discounting Procedure

Discrimination training. To ensure that all of the pigeons could reliably discriminate between one pellet and four pellets before delays were introduced, they underwent discrimination training that involved a left/right (counterbalanced over subjects) spatial discrimination with differential magnitude of reinforcement. Each daily session consisted of five, seven-trial blocks of trials (35 trials total). The first two trials in a block were randomly presented forced trials: one on the left key and one on the right. The remaining trials were choice trials. On forced trials, a white-center stimulus was illuminated to which one peck was required. Responding to the center stimulus resulted in its termination after which, for half of the pigeons, a white stimulus was presented on the left key and one peck resulted in one pellet of reinforcement (delivered while the houselight was illuminated for 2 s). Right forced trials proceeded similarly, except four pellets were delivered. For the other half of the pigeons, the reinforcement contingencies associated with each key were reversed. After the reinforcement sequence, a 60 s intertrial interval (ITI) followed. On choice trials, responding to the center stimulus resulted in its termination after which white stimuli were illuminated on the left and right keys. One peck to either the left or right key darkened

both keys and resulted in the reinforcement associated with the alternative chosen. A limited hold was set such that if a pigeon did not peck the center stimulus within 20 s of its illumination, the trial was counted as an omission and the ITI began immediately. The pigeons were trained on this task until they were reliably choosing the alternative associated with four pellets over one pellet on 80% of the choice trials for three consecutive sessions, after which they were transferred to training with delays.

Training with ascending delays. In training with ascending delays, trials were structured as they were in discrimination training except that a delay to reinforcement was inserted following choice of the four-pellet alternative. The delay remained constant over the block of five choice trials and the delay to reinforcement increased incrementally over blocks of trials. More specifically, in the first block of trials the delay was 0 s, in the second block of trials the delay was 5 s, in the third block of trials the delay was 10 s, in the fourth block of trials the delay was 15 s, and in the fifth block of trials the delay was 20 s. On trials with a delay, following a side-key peck, the side key flashed every 500 ms throughout the delay. During training, the duration of the ITI was adjusted depending on the alternative chosen such that the total trial duration (from trial initiation to the next trial) was always 60 s. All pigeons were trained with this procedure for 25 sessions. After completion of the delay-discounting task, all pigeons were transferred to pretraining for the suboptimal choice procedure.

For the delay-discounting task, the dependent measure was the number of choices of the larger reinforcer per block (maximum five). For each session, a discounting function for each pigeon was obtained by plotting the number of choices of the larger reinforcer as a function of the delay to its receipt. It has been shown that delay discounting functions can be well described by the equation, $V = A/(1 + kD)$, in which V represents the value of the reinforcer, A represents the number of choices of the large reward, D is the delay between the choice response and reinforcement, and k is a free parameter that determines the rate at which V decreases with increases in D (Mazur, 1997).

The ascending delay procedure used to obtain discounting functions in this experiment allowed us to calculate a measure of sensitivity to magnitude as defined by the number of choices of the

large reward at a 0-s delay in the first block of the procedure. Allowing the numerator, A , to vary as a function of how many choices of the large magnitude of reinforcement the pigeon made at a 0-s delay let us determine whether our manipulation affected sensitivity to magnitude or sensitivity to delay. Thus, the equation was fit to the delay-discounting functions for each pigeon first using the equation with A and k as free parameters and second, using the equation with A fixed at 5 (the largest number of choices of the large reward) and k as a free parameter.

As a theoretically neutral measure of delay discounting, area under the discounting curve (AUC) was also calculated for individual pigeons as prescribed by Myerson, Green, and Warusawitharana (2001; see Table 1). To calculate AUC, x and y values were normalized, which resulted in a range of values from 0.0 to 1.0 for the area under each discounting curve; smaller values (close to 0) are indicative of steep discounting (high impulsivity) whereas larger values (close to 1.0 indicate little to no discounting (low impulsivity).

Suboptimal Choice Procedure

Pretraining. The pigeons were trained to peck vertical and horizontal line orientations and yellow, blue, green, and red hues that were singly projected on the left and right response keys. The first peck after 1 s (a fixed interval 1-s schedule of reinforcement; FI 1) turned off the stimulus and delivered two pellets. There were 10 presentations of each stimulus in each session (60 trials per session) for 10 sessions. Upon completion of pretraining, the pigeons were transferred to training on the suboptimal choice task.

Training. At the start of each trial, either a vertical or a horizontal line orientation was presented on one of the side keys. Each line orientation appeared equally often on the left and right. One peck to the line orientation changed the stimulus. If a vertical line was presented (10 trials per session), one peck to it changed the stimulus to red 20% of the time (two trials per session), and upon completion of an FI10-s schedule of reinforcement the stimulus was turned off and 10 pellets were delivered. The remaining 80% of the time that the vertical stimulus was presented, one peck changed it to green (eight trials per session), and after a fixed-time

Table 1
Parameter Estimates for A and k as Well as R -Squared Values for Pigeons Choice on the Delay Discounting Task Using the Equation $V = A/(1 + kD)$ First When A and k are Free Parameters in the Model and Then When A is Constrained to 5.0

Bird no.	$V = A/(1 + kD)$			$V = A/(1 + kD)$			AUC
	A and k are free parameters			A is constrained to 5 and k is a free parameter			
	A	k	R ²	A	k	R ²	
707	5.1384	0.2989	0.8521	5.0000	0.2892	0.8559	0.3350
709	5.0475	0.4925	0.9155	5.0000	0.4873	0.9162	0.2550
725	5.0035	1.3378	0.9851	5.0000	1.3368	0.9851	0.1750
1870	3.6001	5.0315	0.9990	5.0000	7.0237	0.9986	0.1000
703	4.8000	6.7391	0.9994	5.0000	7.0237	0.9994	0.1300
712	4.2071	0.5515	0.9371	5.0000	0.6798	0.9368	0.2150
713	4.4010	1.6723	0.9965	5.0000	1.9151	0.9954	0.1500
716	4.4000	6.1699	0.9999	5.0000	7.0237	0.9992	0.1200

Note. The last column lists area under the curve (AUC) calculations for individual pigeons.

of 10 s (FT10 s) the stimulus was turned off and no pellets were delivered. If a horizontal line was presented (10 trials per session), a peck changed the stimulus to yellow 20% of the time (two trials per session) and to a blue hue 80% of the time (eight trials per session). In each case, upon completion of an FI10-s schedule of reinforcement the stimulus was turned off and three pellets were delivered. The vertical/horizontal line-orientation appeared on both the left and right side keys within a session. The initial link stimuli (vertical or horizontal line orientation) associated with the terminal link stimuli (red/green vs. yellow/blue) were counterbalanced over subjects. A 10-s lit ITI separated the trials.

Each session also included 20 choice trials on which both vertical and horizontal line orientations were presented simultaneously, one on the left key and the other on the right key. A single peck to either initial link stimulus darkened the key not chosen and resulted in presentation of one of the colors associated with that choice with the same probabilities and outcomes as on forced trials. Choice trials were presented randomly among the forced trials. All pigeons received training with this procedure for 25 sessions (see Figure 1).

Results

Delay Discounting

Discrimination training. All of the pigeons reliably chose the alternative associated with four pellets over the alternative associated with one pellet of reinforcement on 80% of the choice trials for three consecutive sessions (mean sessions to criterion: $M = 5.63$, $SEM = 0.80$). Once a pigeon met this criterion, it was transferred to training with ascending delays.

Training with ascending delays. All of the pigeons became sensitive to the delay during delay training. A one-way analysis of variance (ANOVA) conducted on choice of the large reward over the last 5 days of training with session as a factor revealed no upward or downward trend, thus indicating that choice behavior was stable by Session 25 ($F < 1$). Subsequent analysis was conducted on the aggregate data from Sessions 21–25. Using the hyperbolic model with A and k as free parameters, we obtained good fits to the data (see Table 1). We also fit the model to the data with the A parameter constrained to 5. The Akaike Information Criterion (AIC) is a measure of the relative quality of a statistical model—a calculation of goodness of fit based on maximum likelihood that includes a penalty for increasing the number of estimated parameters. The difference in AIC values between the model including both A and k as free parameters in the hyperbolic model and the model including k alone as a free parameter (A constrained to 5) was only 1.62, indicating that including A in the model did not substantially improve the fit. For this reason further analysis will involve the model with k alone as a free parameter (see Table 1 for parameter estimates and hyperbolic fit indexes for individual pigeons). The difference in parameter k between isolate ($M = 4.16$, $SEM = 3.34$) and enriched ($M = 2.28$, $SEM = 3.19$) pigeons was not statistically significant k , $t(6) = -0.81$, $p = 0.44$.

The average plot of choices of the large magnitude of reinforcement as a function of delay for the model with k as the sole free parameter also described the data well, $R^2 = 0.90$; 95% CI (k) = $0.74 \leq k \leq 0.99$ (see Figure 2). Residual analysis of the average of the obtained data by the predicted choices of the

large magnitude of reward $\times$ delay revealed that although there was some apparent systematic variation, overall the linear regression of actual scores by the predicted scores accounted for 94% of the total variance.

AUC was also calculated for individual pigeons (see Table 1). The difference in AUC values between isolate ($M = 0.15$, $SEM = 0.02$) and enriched ($M = 0.22$, $SEM = 0.05$) pigeons was not statistically significant k , $t(6) = 1.14$, $p = .30$. Importantly, individual pigeons showed considerable variability in the rate at which they discounted the larger reward (k value) and in their AUC values, making it meaningful to examine the correlation between these measures of impulsivity (k value and AUC) and our second measure, suboptimal choice. There was a strong correlation between k values and AUC calculations ($r = -0.80$, 95% CI (r) = $-0.96 \leq r \leq -0.16$; $t(6) = 3.30$, $p < 0.05$).

Acquisition of Suboptimal Choice

In line with the results of earlier research (Laude et al., 2012; Pattison et al., 2013), pigeons in the present experiment showed an initial preference for the *optimal* alternative and after about eight sessions began to show a reversal of their initial preference. By the end of training most pigeons showed a clear preference for the suboptimal alternative. Although the pigeons in the enriched condition acquired the suboptimal choice somewhat slower than the pigeons in the isolate condition, a two-way, mixed-effects ANOVA conducted on suboptimal choices, with session as a within-subject factor (1–25) and housing condition (enriched and isolated) as a between-subjects factor did not reveal a significant main effect of housing condition, $F(1, 6) = 1.56$, $p = 0.26$. A significant main effect of session was found, $F(24, 144) = 7.28$, $p < 0.01$, indicating that the pigeons' preferences were changing as a function of training, however, the housing $\times$ session interaction was not significant $F < 1$. Because differences in suboptimal choice between socially enriched and isolate pigeons were not observed, the data were pooled over groups for further analyses.

When suboptimal choices from the last 5 days of training were pooled for each pigeon and compared with the mean k -value from the last 5 days of training on the discounting task for each pigeon, a significant positive correlation was observed, $r = 0.84$, 95% CI (r) = $0.34 \leq r \leq .97$; $t(6) = 3.81$, $p < 0.05$ (see Figure 3 left). This means that greater rates of discounting as indexed by k (increased impulsivity) were associated with increased choice of the suboptimal alternative.

There was also a significant negative correlation between AUC calculations and suboptimal choice, $r = -.70$, 95% CI (r) = $-0.94 \leq r \leq .01$; $t(6) = -2.39$, $p = .05$, such that smaller AUC values (indicative of greater impulsivity) were associated with increased suboptimal choice (see Figure 3 right).

Given the significant correlation between k -value and suboptimal choice, we performed a median split of the k -values and compared the percentage choice of the suboptimal alternative as a function of session for the high and low k -value groups. It should be noted that the median split on AUC values resulted in the same classification of subjects into high and low impulsivity groups and, thus, the same results would have been obtained using AUC values in the subsequent analyses.

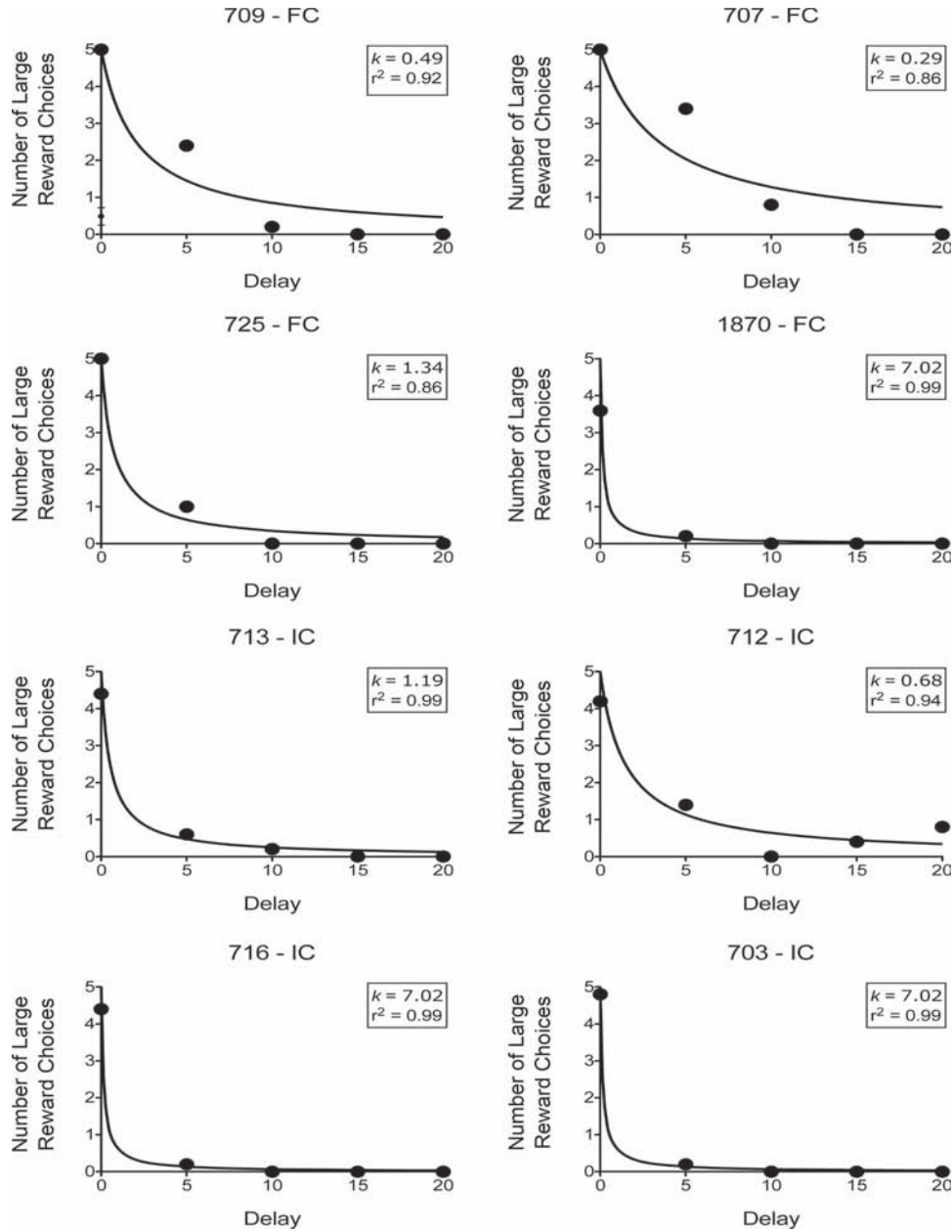


Figure 2. Graphical representations of model $V = A/(1 + kD)$ in which A is constrained to 5.0 and k is a free parameter fit to individual delay-discounting functions. The horizontal axis shows the delays used during training. The vertical axis shows the number of opportunities on which the pigeon chose the larger reinforcer at each of the delays.

A two-way, mixed-effects ANOVA on suboptimal choice, with session as a within-subject factor (1–25) and k -value (high vs. low) as a between-subjects factor, revealed a main effect of impulsivity, $F(1, 6) = 7.97$, $p = 0.03$. There was also a significant main effect of session, $F(24, 144) = 8.91$, $p < 0.01$, and a significant k -value $\times$ session interaction, $F(24, 144) = 2.35$, $p = .01$ (see Figure 4). To determine the source of the interaction, we pooled the data from the last five sessions of suboptimal choice training and conducted a two-sample t test. The result indicated that there was a significant difference in suboptimal choice between the high

and low k -value pigeons, $t(6) = 4.60$, $p < 0.01$, $d = 1.65$, 95% CI (d) = $0.94 \leq d \leq 5.47$.

Discussion

The purpose of the present experiment was to test the hypothesis that impulsivity, as measured by a delay-discounting function, is associated with suboptimal choice. This hypothesis was based on findings in the human gambling literature that report a relationship between impulsivity and degree of gambling severity, as well as an

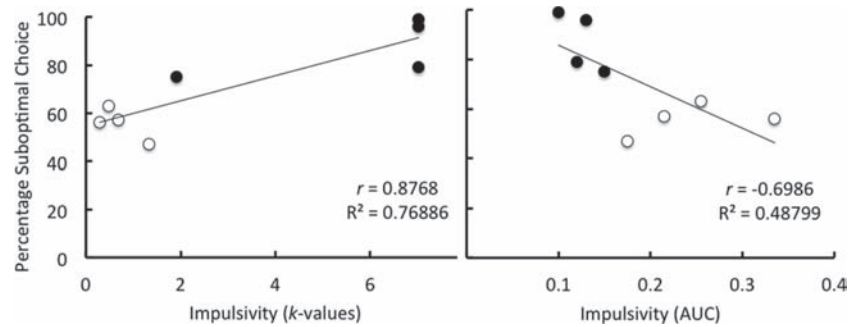


Figure 3. First panel: Correlation between k -values (discounting functions fit to the hyperbolic model $V = A/(1 + kD)$ in which A is constrained to 5 and k is a free parameter) and suboptimal choice. Second panel: Correlation between AUC calculations and suboptimal choice.

effect of increased motivation and social isolation on the two tasks. Consistent with this hypothesis, we found that sensitivity to delay in a temporal discounting choice procedure was positively correlated with degree of suboptimal choice in our gambling-like task. Although with extended discrimination training, all pigeons showed an increase in suboptimal choice, the increase for the pigeons that showed a steep slope in the discounting function (high k -value) was significantly larger than for the pigeons that showed a relatively flat slope in the discounting function (low k -value), indicating that the rate of acquisition was faster and the degree of suboptimal choice was greater for pigeons in the high k -value group. Results obtained using a theoretically neutral measure of delay-discounting (AUC) produced a pattern of results that could be interpreted in the same way. These findings suggest that an important component of impulsivity for pigeons that choose suboptimally in our task, like humans who report that they gamble, is a preference for a smaller-sooner over a larger-later reward.

Although we did not observe significant differences in choice behavior between socially enriched and isolated groups comparable with that found by Pattison et al., (2013) in the present experiment, there was a tendency in that direction. Several differences between the original social enrichment experiment and the present experiment may account for the smaller effect in the present experiment. The original social enrichment manipulation used a suboptimal choice procedure that involved the manipulation

of probability of reinforcement rather than magnitude of reinforcement. In addition, homing pigeons were used by Pattison et al., whereas the present study was conducted with white Carneau pigeons. Thus, differences in sociability or in-group dynamics could also explain differences in results. For example, if the homing pigeons were more socially interactive, we might expect the manipulation to have had a greater effect. As for the impulsivity measure, three of the four socially-enriched pigeons were in the low k -value group and three of the four isolated pigeons were in the high k -value group. This raises the possibility that statistical significance would have been reached had the study included more subjects.

Given that the suboptimal choice and delay discounting tasks are related but the procedures are quite different, one might speculate about the mechanism that relates them. Results from the present study suggest that the degree to which pigeons process signals for reinforcement and nonreinforcement may be affected by individual differences in the pigeons' levels of impulsivity. The question is why impulsivity should affect the pigeons' choice of the suboptimal alternative in the gambling-like task. It is likely that it is related to the conditioned reinforcers. When the magnitude of reinforcement is manipulated (Zentall & Stagner, 2011), the larger reinforcement (10 pellets) predicted by the signal for reinforcement associated with the suboptimal alternative makes it a better conditioned reinforcer than the signals for reinforcement associated with the optimal alternative (three pellets). Similarly, when the probability of reinforcement is manipulated (e.g., Stagner & Zentall, 2010), the higher probability of reinforcement (1.0) predicted by the signal for reinforcement associated with the suboptimal alternative makes it a better conditioned reinforcer than the signal for reinforcement associated with the optimal alternative (.5). Thus, in both cases, pigeons will tend to choose suboptimally because the immediate outcome of choice is either the conditioned reinforcer associated with the optimal alternative or a stronger conditioned reinforcer associated with the suboptimal alternative. For this reason, the pigeons (and likely the gamblers) appear to be comparing the value of the conditioned reinforcers associated with the two alternatives, rather than the overall probability or amount of reinforcement associated with the two alternatives.

These results suggest that pigeons that choose suboptimally (and likely human gamblers as well) have an impaired ability to accurately integrate reinforcement and the absence of reinforcement

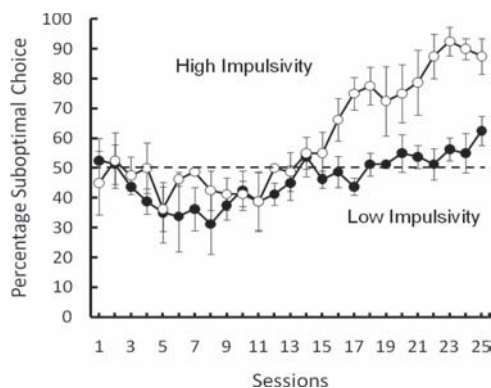


Figure 4. Percentage choice of the suboptimal alternative as a function of training session for high and low impulsivity groups.

over trials, which may be especially difficult if the individuals have a short *time horizon* (Krebs & Kacelnik, 1984). To accurately assess the overall probabilities of reinforcement, the subject must accumulate the frequencies of the outcomes associated with each terminal link, and there is converging evidence that they are impaired in their ability to do so. We have found that when the suboptimal choice task is modified such that both alternatives yield equally strong conditioned reinforcers (i.e., each conditioned reinforcer is associated with 100% reinforcement) but for the one alternative the probability of the occurrence of the conditioned reinforcer is .20 whereas for the other alternative the probability of the occurrence of the conditioned reinforcer is .50, pigeons do not appear to be able to discriminate between those probabilities (i.e., they are indifferent between the two alternatives; Stagner, Laude, & Zentall, in press). Integrating these frequencies may be especially difficult for pigeons with steep discounting functions (i.e., high k -values).

Consistent with this memory-based hypothesis, Killeen (2011) has proposed a model based on memory for delayed reinforcers that mediate choice. Killeen suggests that the residual memory of the response that produced the reinforcer is reduced with time and that accounts for the effects of reinforcer delay on behavior. If temporal discounting provides an index of memory for delayed reinforcement, pigeons with higher baseline levels of impulsivity may have poorer memories for delayed reinforcers and poorer memory may impair their ability to accumulate the consequences of choice over trials. In fact, there is evidence that suggests that such a relationship exists in humans (Hinson, Jameson, & Whitney, 2003) and that working memory deficits are related to gambling (Leiserson & Pihl, 2007). Thus, deficits in working memory may underlie discounting measures of impulsivity and suboptimal choice.

Despite the appeal of the conditioned reinforcement hypothesis, it fails to consider the expected conditioned inhibition that should accrue to the stimulus associated with the absence of reinforcement. If the stimulus associated with the absence of reinforcement is inhibitory, it should come to control a tendency opposite that of the conditioned reinforcer and should decrease choice of the suboptimal alternative (Rescorla, 1969). Conditioned inhibition should be particularly strong when the probability of reinforcement is low (.20) and the probability of nonreinforcement is high (.80); yet Stagner and Zentall (2010) found a strong (97%) preference for the suboptimal choice under just such conditions. Thus, it appears that for pigeons with high k -values, as well as for humans who gamble, signals for reinforcement (winning) appear to have greater positive value than they would be expected to have, especially considering that signals for the absence of reinforcement (losing) occur much more often (Molet et al., 2011; Stagner & Zentall, 2010; Zentall & Stagner, 2011). In the gambling literature on reward and punishment sensitivity for pathological gamblers, parallel findings exist, which reveal that gamblers have higher immediate reward sensitivity, as compared with controls (Goudriaan, Oosterlaan, de Beurs, & van den Brink, 2006; Petry, 2001). Furthermore, reduced conditioned inhibition to losses has also been proposed to account for human gambling behavior (Blanco, Ibáñez, Sáiz-Ruiz, Blanco-Jerez, & Nunes, 2000; Breen & Zuckerman, 1999).

One possibility for why the stimulus associated with the absence of reinforcement may not have become a strong conditioned inhibitor is that the pigeons may have turned away from it when it

appeared as a localized stimulus. For example, there is evidence that the effectiveness of conditioning for pigeons depends on the time that the pigeon spends in the presence of the stimulus (Roberts, 1972). To test the hypothesis that pigeons may reduce the effectiveness of the signal for nonreinforcement may be reduced because the pigeons turn away from it, Stagner, Laude, and Zentall (2011) used a diffused houselight in place of the localized stimulus associated with the absence of reinforcement (the S-). If reduced observation of the stimulus associated with the absence of reinforcement was responsible for undervaluing its inhibitory effect, then the preference for the lower probability of reinforcement alternative should have been reduced or eliminated when the houselight was the stimulus associated with the absence of reinforcement. However, we found that those pigeons showed a preference for the suboptimal alternative that was as strong as it was for both a control group for which the houselight served as the signal for reinforcement and a standard group for which both stimuli were localized stimuli. These results suggest that reduced inhibition due to reduced observation of the S- stimulus was probably not the reason that the pigeons preferred the suboptimal alternative. Given these results, peripheral sensory inattention (the absence of orienting behavior) is not likely to be the mechanism responsible for the absence of inhibition to the S- and, thus, for the preference for the suboptimal alternative.

Thus, it is likely that a more central form of attention is involved in this phenomenon. Attentional differences to the S- stimulus could depend on a pigeon's level of impulsivity. It is possible that low k -value animals may better attend to the S- stimulus than high k -value animals, which may affect the acquisition of conditioned inhibition. In any case, the stimulus associated with the absence of reinforcement did not acquire sufficient inhibition to counteract the conditioned reinforcement associated with the S+, resulting in less optimal choice. In fact, there is evidence that animals that are more impulsive show a reduced ability to acquire conditioned inhibition (Migo et al., 2006). Thus, for pigeons that choose suboptimally, like humans who gamble, losses appear to contribute much less conditioned inhibition than they should according to reinforcement theory (van Holst, van den Brink, Veltman, & Goudriaan, 2010).

If similar mechanisms underlie temporal discounting for gains and losses, and there is some evidence that they do (see Green & Myerson, 2010), another possibility is that delayed aversive outcomes are more steeply discounted for pigeons with high k -values (i.e., they have less of a negative effect), which would then fail to deter choice of the suboptimal alternative. Furthermore, it has been suggested that when gamblers take a mental accounting of the sum of immediate (undiscounted) gains and delayed (discounted) losses, the net value of gambling tends to be substantially positive, resulting in rapid acquisition and maintenance of gambling behavior (Petry & Madden, 2010). Humans who do not gamble may be more affected by a string of losses if they discount delayed negative outcomes at a lower rate and this may be sufficient to discourage gambling behavior. Being affected by a string of losses implies memory for losing outcomes across repeated gambles (*string theory*; Rachlin, 1990; Rachlin, 2000). Again, we see the possibility that impaired memory, which may be particularly characteristic of impulsive individuals, could lead to a failed ability to integrate and maintain outcome frequency over trials, resulting in continued gambling.

Although the results of the present experiment suggest that impulsivity is implicated in choice of the suboptimal alternative, the underlying mechanism involved in suboptimal choice is unclear. Whether choice of this alternative results from an inability to resist the attraction of the immediately available but only occasional signal for the high valued outcome, poor memory for the accumulated outcomes of choice responses, a general lack of inhibitory control, or some combination of these is still unresolved (Hoch & Loewenstein, 1991; Zuckerman, 1994).

The results of the present study indicate that the choice task with pigeons involving a choice between a low-probability, high-payoff alternative over a high-probability, low-payoff alternative provides a worthy analog to suboptimal decision making observed in human gamblers. In the present experiment, pigeons with higher baseline levels of impulsivity, as indicated by their performance on the delay-discounting task, show greater degrees of suboptimal choice. This finding provides further evidence in support of the hypothesis that impulsivity acts as a proximal mechanism that functions to increase attraction to the stronger conditioned reinforcer associated with the suboptimal alternative, resulting in an increased preference for that alternative. These results suggest a direction for determining the mechanisms underlying suboptimal choice with the gambling-like task used in the present research, as well as mechanisms underlying impulsive choices made by pathological gamblers.

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