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THE BALLOON ANALGOUE RISK TASK AND
BEHAVIORAL CORRELATES IN PIGEONS

THESIS

A thesis submitted in partial fulfillment of the requires for the
degree of Master of Science in the College of Arts and
Sciences at the University of Kentucky

By

Aaron Paul Smith

Lexington, Kentucky

Director: Dr. Thomas R. Zentall, Professor of Psychology

Lexington, KY

2015

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ABSTRACT OF THESIS

THE BALLOON ANALGOUE RISK TASK AND BEHAVIORAL CORRELATES IN PIGEONS

Individuals experience risk ubiquitously, but measuring risk taking is difficult. The balloon analogue risk task (BART) was developed in order to assess risk taking through having subjects press a key that accrues reward but also risk losing all reward with each press. In humans, greater responding in this task is associated with other maladaptive risk taking behaviors. The present research modeled this relationship in pigeons due to their previously shown propensity towards risk taking behavior. Experiment 1 used an unsignaled balloon task in which losing could only occur after 5 pecks. Results showed below optimal performance with greater pecks associated with faster acquisition of risk taking in the suboptimal choice task and evidence of modulation by delay discounting measures. Experiment 2 signaled the number of pecks with colors and tested multiple hoppers as a reinforcement modality to increase performance. Results showed only signaling the number of pecks improved performance and was related to performance in the high risk BART task. Both the low and high risk variants were associated with slower suboptimal choice acquisition and again had evidence of modulation by delay discounting measures. Potential shared underlying mechanisms are discussed.

KEYWORDS: Risky choice, impulsivity, suboptimal choice, delay discounting, pigeon

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September 3, 2015

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BEHAVIORAL CORRELATES IN PIGEONS

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SECTION ONE: INTRODUCTION

Risk as a Construct

Risk is a ubiquitous facet of life that all individuals must consider, yet the ways in which risk is dealt with can vary. Risk taking behaviors have been defined as those that involve balancing potential gains and losses in both the short- and long-term (Skeel, Neudecker, Pilarski, & Pytlak, 2007). While this definition of risk taking encompasses behaviors of both positive and negative consequences, behaviors with negative associations have tended to receive more attention in the psychological literature. For example, individuals who take greater risks have been associated with alcohol abuse (Ferne, Cole, Goudie, & Field, 2010), smoking (Lejuez, Aklin, Jones, et al., 2003), self-reports of adolescent risky behaviors (Lejuez, Aklin, Zvolensky, & Pedulla, 2003), and MDMA (ecstasy) use (Hopko et al., 2006).

Risk taking is a difficult construct to measure (see Fox & Tannenbaum, 2011). It has often been assessed in relation to constructs such as sensation seeking, or an individual's desire to seek out novel, varied, and intense experiences (Roberti, 2004; Zuckerman, 1971) and impulsivity, a multi-dimensional construct that often refers to an individual's inability to inhibit motor responses or delay gratification (Evenden, 1999; Monterosso & Ainslie, 1999). Both sensation seeking and impulsivity also have popularized and widely used methods of measurement. Sensation seeking is often measured using the self-report sensation seeking scale (Zuckerman, 1971), while impulsivity is also often measured through self-report scales (Eysenck & Eysenck, 1978; Patton, Stanford, & Barratt, 1995), or behavioral tasks such as the delay discounting (DD) task (Mazur, 1987). Through these measures, both sensation seeking and impulsivity have shown indirect associations with risk behaviors (see Roberti,

2004; Verdejo-García, Lawrence, & Clark, 2008 for a review); however, recent research has been interested in attempting to distinguish between these similar constructs (e.g. Collado, Felton, MacPherson, & Lejuez; Lauriola, Panno, Levin, & Lejuez, 2014).

Directly measuring risk taking behavior or propensity, however, has not yet achieved the same relatively standardized procedures of measurement (Fox & Tannenbaum, 2011). Measuring risk taking has often been done using behavioral choice tasks that offer a choice between an option that yields large wins with frequent losses against an alternative with smaller wins and fewer losses (e.g. Marshall & Kirkpatrick, 2013; Stagner & Zentall, 2010). One such example of this is probability discounting, in which an individual is given the choice between a certain option of a smaller magnitude against a larger magnitude option that is probabilistically given at varying probabilities (Rachlin, Raineri, & Cross, 1991).

A second example is the Iowa, or Bechara, Gambling Task (IGT; Bechara, Damasio, Damasio, & Anderson, 1994), which has become one of the most popular tasks to study risk taking behavior. In this task, participants choose among four decks of cards, two being ‘good’ (with positive expected values) and two ‘bad’ (with negative expected values). In the IGT, participants must forgo the bad decks that have more immediate and larger gains with greater losses in favor of the good decks that have smaller rewards with fewer losses. This task has shown relevance to gambling behaviors (see Brevers, Bechara, Cleeremans, & Noël, 2013, for a review); however, recent research has questioned its validity at measuring risk taking, particularly in normal populations (e.g. Lin, Song, Chen, Lee, & Chiu, 2013; Steingroever, Wetzels, Horstmann, Neumann, & Wagenmakers, 2013). One primary concern with the IGT is its poor test-retest reliability as participants will often switch preference strategies with continued experience, possibly indicating why correlations with other tasks

change depending on experience with the task (Xu, Korczykowski, Zhu, & Rao, 2013). In addition, this task has been less successful at assessing normal, healthy participants, who have been shown to perform marginally more optimal than clinical populations (Steingroever et al., 2013).

The Balloon Analogue Risk Task (BART)

As an alternative measure of risk taking behavior, Lejuez et al. (2002) recently developed the balloon analogue risk task (BART), in an attempt to gain a better behavioral measure of risk taking.

The BART (Lejuez et al., 2002) requires individuals to press a button in order to inflate a virtual balloon. Each response, or pump, on this button increases the size of the balloon and subsequently adds a set amount of reward being tracked by a local reward tracker for that trial. With each pump, however, there is also an increasing risk of the balloon ‘popping’ or ‘exploding,’ after which all of the reward accrued over that trial is lost. In order to obtain the reward prior to losing it, the individual must press a separate cash out or claim button to end the trial, claim the accrued reward, and get a new balloon. If the individual collects the reward prior to the balloon popping, the reward is added to a global reward tracker that accounts for the total reward earned over a session and is safe from further balloon explosions.

In the original human task the balloon has a maximum of 128 possible pumps where the risk is incremented through a list in which one number out of the 128 codes the balloon to explode. As such, the balloon’s chance of popping increments by $1/128$, $1/127$, $1/126$, etc. The primary dependent measure is usually the average number of adjusted pumps, which averages the pumps only on successful trials where the reward was collected. Lejuez et al.

(2002) argued that this measure is superior to averaging the total number of pumps as trials where the balloon explodes restrict any further responses past the point of explosion. However, other measures such as reward earned (Skeel et al., 2007), variability in responding (Jentsch, Woods, Groman, & Seu, 2010), and changes in responding over a session (Humphreys, Lee, & Tottenham, 2013; Lejuez et al., 2002) have also been used. Multiple balloons of different colors have also been used, often with different probabilities of exploding (e.g. Fukunaga, Brown, & Bogg, 2012; Lejuez et al., 2002; Mitchell, Schoel, & Stevens, 2008) or explode at different fixed numbers of pumps (Humphreys et al., 2013).

Predictive Validity. These measures of BART risk taking have also shown validity in assessing particular risk behaviors. For example, average number of adjusted balloon pumps have been associated with risk taking behaviors such as alcohol abuse (Ferne et al., 2010), smoking (Lejuez, Aklin, Jones, et al., 2003), self-reports of adolescent risky behaviors (Lejuez, Aklin, Zvolensky, et al., 2003), risky sex (Lejuez, Simmons, Aklin, Daughters, & Dvir, 2004), attention deficit hyperactivity disorder, operant defiant disorder (Humphreys & Lee, 2011), and MDMA use (Hopko et al., 2006), while money earned was associated with alcohol consumption (Skeel et al., 2007). In addition, the BART has also shown moderate test-retest correlations (White, Lejuez, & de Wit, 2008; Xu et al., 2013). Although some cases of significant increases in retest pumps have been reported (Weafer, Baggott, & de Wit, 2013), the test-retest correlations remained high ($r = .79$), suggesting that the rank order of individuals remained close to the same and that the task may be tapping into a relatively stable facet of risk taking behavior. The findings are not consistent, however, as some reports of BART risk taking have found no association with risk behaviors (Dean, Sugar, Helleman, & London, 2011; Szrek, Chao, Ramlagan, & Peltzer, 2012), and may be more

accurate when used in conjunction with related constructs such as sensation seeking and impulsivity (Bornovalova et al., 2009). As such, continued research into the validity of the BART as a diagnostic measure for predicting risk taking behaviors is necessary to elucidate these findings.

Behavioral Mechanisms. While experiments looking at BART risk taking and its associations have gained popularity, parametric manipulations of task variables have been less explored. The most consistent finding with the BART is that individuals tend to be relatively risk averse (Campbell, Samartgis, & Crowe, 2013; Fukunaga et al., 2012; Lauriola et al., 2014; Lejuez, Aklin, Jones, et al., 2003; Lejuez, Aklin, Zvolensky, et al., 2003; Lejuez et al., 2002; Rolison, Hanoch, & Wood, 2012; White et al., 2008), meaning that the number of responses made on a given trial tends to be less than what would maximize reward across the session. Indeed, a meta-analysis of BART risk taking found that individuals tended to pump on average only 24-48 times where the optimal number of pumps (usually half) was 64 (Lauriola et al., 2014). This aversion to risk also increases when the magnitude of reward given for each pump is raised (Bornovalova et al., 2009; Vigil-Colet, 2007), suggesting that, in line with prospect theory, decision making in the BART tends to be driven by a desire to reduce losses (Kanehman & Tversky, 1979).

BART risk taking is also further complicated due its often found associations with impulsivity and sensation seeking. For example, Vigil-Colet (2007) found that a subtype of self-reported impulsivity pumped more often when the risk of losing was low and also earned more points. Additionally, another study found that when reward magnitudes were increased from 1, to 5, to 25 cents, self-reported individuals high on a combined impulsive and sensation seeking scale showed less of a reduction in the number of both total and adjusted

pumps (Bornovalova et al., 2009), to which the authors suggested may be due to either a reduced sensitivity to losses or a more balanced assessment of risk. This study is also congruent with another (Humphreys et al., 2013) that looked at self-reported sensation seeking levels in conjunction with 3 balloons, two of which had fixed explosion points while a third had a variable explosion point. Their results indicated that individuals high on sensation seeking tended to pump more on average and experience more balloon explosions. However, a subset of these sensation seekers also showed greater learning of the task between the first and last third of the session, ending with a greater total number of points and reduced number of explosions. While associations between the BART and impulsivity / sensation seeking scores are not always found (e.g. Hopko et al., 2006; Xu et al., 2013), a recent meta-analysis with over 2,000 participants found significant, although small, associations with each construct (Lauriola et al., 2014). Thus, while potentially associated with each other, it is still possible that the BART may still be a separate construct (Lejuez, Aklin, Jones, et al., 2003; Lejuez, Aklin, Zvolensky, et al., 2003).

This potential indirect association with impulsivity / sensation seeking seems to often influence the BART through increasing the number of BART pumps (Bornovalova et al., 2009; Humphreys et al., 2013; Vigil-Colet, 2007), which can translate to increased rewards (e.g. Humphreys et al., 2013). Still, increased pumps on the BART task tends to be framed negatively due to its associations with maladaptive behaviors. In the context of most studies looking at both healthy control and target populations, though, at risk populations pump closer to the optimal amount (see Lauriola et al., 2014). Indeed, many studies are beginning to discuss this apparent paradox in which normally maladaptive risk takers can show

adaptive risk taking with the BART (Bornovalova et al., 2009; Campbell et al., 2013; Dean et al., 2011; Humphreys et al., 2013; Rolison et al., 2012; Vigil-Colet, 2007).

Half of the maximum number of pumps is usually the optimal number of responses in the BART to maximize reward; however, this requires that an individual also be willing to experience many losses in order to learn this as an individual will lose 50% of the time with that many pumps. As such, if an individual is loss averse and unwilling to experience that many losses, learning that higher pumps nets greater rewards at the cost of more frequent losses (the optimal level of responding) may never happen (Rolison et al., 2012). This trade-off bears similarities to an exploration versus exploitation strategy (see Cohen, McClure, & Angela, 2007 for a review). Exploitation refers to the continued choice of a known alternative, whereas exploration refers to the sampling of different alternatives. In the context of the BART, individuals who are risk averse may often exploit, or continue to choose, lower values of BART pumps, never exploring the higher values in order to learn the greater net payoffs. This then creates an environment in which greater risk taking can be adaptive (Bornovalova et al., 2009; Humphreys et al., 2015; Humphreys et al., 2013; Vigil-Colet, 2007) despite its associations with other maladaptive behaviors.

Another potential factor in line with this idea is diminishing marginal value (e.g. Shanteau & Troutman, 1992). As suggested by Lejuez et al. (2002), each additional reward that is gained through pumping the balloon adds proportionally less reward than the pump before. For example, the second pump takes the individual from having five cents to ten cents, or a 100% increase in reward value. The third pump then adds the same amount of reward, however only increasing the total reward earned by 50%. Each successive pump is perceived as less valuable due to the previously accrued reward. At the same time, the risk

of losing all of the accrued reward is increasing. Thus, each subsequent response reinforces the individual with an ever diminishing reward value while the risk of losing all of the accrued reward continues to steadily increase, potentially further adding to the propensity for individuals to exploit lower BART pump values.

Neurological Mechanisms. In line with the idea of sensitivity to losses, recent functional magnetic resonance (fMRI) and functional near-infrared spectroscopy (fNIRS) studies have used the BART to examine this question. Rao, Korczykowski, Pluta, Hoang, and Detre (2008) sought to determine which brain regions were active in the risk component of the BART by having two variations under fMRI. The first variation, the active BART, was similar to the normal BART except that the maximum pumps were capped at 12 while the second variation had participants watch as a computer produced the number of pumps and the outcome for that trial. This second variation, they argued, was analogous to passively experiencing the BART. In the active BART, dopamine mesolimbic structures such as the ventral tegmental area (VTA), striatum, anterior insula, dorsolateral prefrontal cortex (dlPFC), and anterior cingulate cortex (ACC) all showed high activity, while the passive BART showed no brain region activations. In addition, the striatum, often implicated in reward valuation, had greater activation during losses rather than wins. This, the authors suggested, may have been due to prediction error from the balloon unexpectedly bursting as opposed to an expected cash out during a win trial, possibly contributing to a heightened salience of loss trials.

A second study by Cazzell, Li, Lin, Patel, and Liu (2012) using fNIRS supported the findings by Rao et al. (2008), but also found that the males in their study pumped more on average, thereby losing more often, and showed reduced activity in the left dlPFC. Finally, a

study by Fukunaga et al. (2012) found that participants responding to an altered BART with a maximum 12 responses using fMRI showed decreased signaling in the right ACC and bilateral inferior frontal gyrus (IFG), and increased activity when subjects chose to cash out. This, the authors argued, implicated both the ACC and IFG in risk aversion. Thus, if an individual had reduced sensitivity in the dlPFC, ACC, or IFG, this may in part explain why they pump more often in the BART.

Animal analogues of BART risk taking.

Rat models. Animal analogues have also contributed to the understanding of the BART task. Currently, only two studies have been published using animal models of the BART, both with rats (Ashenurst, Seaman, & Jentsch, 2012; Jentsch et al., 2010). In the first of these tasks (Jentsch et al., 2010) rats responded to two levers, an add lever that accumulated one pellet of food per press and a cash out lever that immediately produced the accumulated pellets equal to the add lever presses. Conditions where risk was present for pressing the add key were signaled by illuminating the house light with a maximum of 10 presses while no risk sessions were signaled with a localized light and the number of responses only capped at 100 add lever presses. Popping the balloon resulted in a darkened time out period of 5 s, during which responding was not possible. The risk associated with the add lever was manipulated from 11.1% per press to 16.7% per press. Finally, the probability of the cash out key actually delivering the accumulated reward was manipulated from 100% to 50% and then 33%.

Jentsch et al. (2010) found that, as in humans, the rats were largely risk averse, only responding around 2.8 times on average instead of the more optimal higher numbers. When the probability of the cash out key delivering reinforcement was decreased, the number of

presses per trial increased to approximately 3 per trial, while increasing the risk per add key press subsequently decreased the average number of presses. These manipulations showed the rats were sensitive to the changes in probability of both risk and reinforcement. A separate group of rats were then tested with transiently inactivated orbitofrontal cortex regions and found a significant reduction in the number of presses per trial, implicating yet another brain region in BART performance measures. Ashenurst et al. (2012) later conducted an experiment of similar design with different strains of rats and found large degrees of variance in risk taking were explained by the different strains, suggesting that risk taking within this task may be attributable to certain traits or phenotypes.

Pigeon models. To date, there have been no studies published with pigeons using the BART, yet they may be an appropriate model of risk taking behavior. For example, pigeons share a primary sense of sight with humans, which allows for the examination of visual cues and a greater variety of stimuli for behavior to come under control of. Additionally, pigeons have also been shown to reliably ‘gamble,’ or prefer a discriminative ‘jackpot’ stimulus that predicts 10 pellets of food 20% of the time over non-discriminative stimuli that each predict 3 pellets of food 100% of the time (Zentall, 2011; Zentall & Stagner, 2011). This effect in the so called suboptimal choice task appears to stem from a diminished sensitivity to the frequent losses associated with the jackpot stimulus (Laude, Stagner, & Zentall, 2014) as well as an over valuation of the conditioned reinforcer’s value associated with it (Smith & Zentall, under review; Stagner, Laude, & Zentall, 2012; Zentall, Laude, Stagner, & Smith, 2015), both of which share similarities to human gamblers (van Holst, van den Brink, Veltman, & Goudriaan, 2010). Thus, pigeons may serve as a good animal model for BART risk taking behaviors.

Also, while no widely used analogues exist within the pigeon for sensation or novelty seeking, there are for impulsivity measures. Specifically, impulsivity can be measured through the DD task which pits a small reward available soon (the SS) against a larger reward available later (the LL). In this task, the degree to which the animal forgoes the larger reward in favor of the smaller reward at various LL delays is indicative of the individual's rate of discounting, or the rate at which the delayed reward is devalued (see Odum, 2011; Reynolds, 2006, for a review). Like humans, this rate of discounting, or k value, has been posited as trait impulsivity (Odum, 2011) and has been shown to be related to risky choice in rats (Kirkpatrick, Marshall, & Smith, 2015) and positively correlated with suboptimal risky choice in pigeons (Laude, Beckmann, Daniels, & Zentall, 2014). Additionally, when tested under attempts to make conditions as similar as possible, pigeons have been shown to have relatively heightened levels of discounting to both humans and rats (Tobin & Logue, 1994).

Rationale and Hypotheses

The current evidence thus suggests that pigeons may be a good animal analogue to test both BART risk taking and its association with impulsivity levels. Similar to human experiments, the present study set up two 'screens': one for risk taking behaviors in the BART and one for impulsivity levels in the delay discounting task. Additionally, to test for associations with other maladaptive behaviors, the suboptimal choice task can serve as the pigeon analogue of human gambling as an outcome variable.

In addition to the BART, however, the present experiment assessed a measure for how pigeons would behave in this task under conditions of low risk. Similar to the no risk session in Jentsch et al. (2010) and balloons with fixed explosion points in Humphreys et al.

(2013), the so called balloon emotional learning task (BELT) from the latter study allows for the examination of the incentive to respond for greater amounts of reward when the overall risk is low by fixing the balloon's explosion point.

Given the findings from the previous research, four hypotheses were made. First, that responding under conditions of low risk in the BELT task would be associated with responding under greater risk in the BART task. Second, that the degree of risk taking within the BART task and reward maximization in the BELT task would be associated with risk taking in the separate suboptimal choice task. Third, that impulsivity as assessed by the delay discounting task would be related to both the BART and suboptimal choice tasks. Finally, the fourth was that the BART and delay discounting tasks may have an additive or interaction effect in their predictive validity on the suboptimal choice task due to the previously found correlations between each of the tasks.

Section 2: Experiment 1

Method

Animals. 10 experimentally non-naïve White Carneaux pigeons purchased from the Palmetto Pigeon Plant (Sumter, SC) were used in the experiment. One pigeon had previous experience with the delay discounting and suboptimal choice tasks (Laude, Beckmann, et al., 2014). The pigeons were approximately five years old at the onset of behavioral testing. They were maintained on a restricted diet of 85% of their ad libitum weight with free access to grit and water. The pigeons were housed in wire cages measuring $28 \times 38 \times 30.5$ cm in a colony room kept on a 12 hour light-dark cycle (lights off at 7 p.m.).

Apparatus. All phases of the experiment were conducted in a Med Associates (St. Albans, VT) modular operant chamber (ENV-008) measuring approximately $30.5 \times 25.5 \times 33$ cm inside of a noise attenuating box measuring approximately $65 \times 40.5 \times 55$ cm. The chamber consisted of a horizontal row of three round (2.54 cm diameter) response keys approximately 5 cm apart from each other, behind which was a 12-stimulus inline project (Industrial Electronics Engineering, Van Nuys, CA) that projected both colored and shape stimuli. Reinforcement was delivered to a magazine tray at the base of the response panel from a pellet dispenser (ENV-45) mounted behind the response panel, and a 28 V, .1 A houselight was centered over the middle of the chamber. A computer running Med-PC IV (Tatham & Zurn, 1989) controlled the experiment with a 10-ms resolution.

Procedure.

Pre-training. The pigeons first experienced two sessions of habituation training to the operant chamber for 30-m with the houselight on, but no other events. After habituation training, eight sessions of magazine training were given on a 30-s variable time (VT)

schedule ranging from 1-60 s. The houselight remained on except for a 5-s dark intertrial interval (ITI) between reinforcements. The pigeons were then trained for two sessions on a fixed ratio (FR1) to a center white stimulus followed by two sessions to a right green stimulus for 60 trials. Following FR1 training, the pigeons completed 10 sessions of FR training to both stimuli. These sessions were identical to the first FR training sessions except that the response requirement on the right green stimulus was incremented by one after the completion of two successive sessions, such that on the last day of training the pigeons completed an FR5 on the right green stimulus for 40 trials and an FR1 on the center white stimulus for 10 trials.

BELT. The BELT task immediately followed pretraining. Trial onset began with the illumination of the houselight, a white center stimulus (the cash out key) and a right green stimulus (add key). The pigeons were required to respond at least once to the add key and up to five times after which a response to the cash out key would extinguish the stimuli and deliver pellet reinforcements equal to the number of pecks made. The houselight remained illuminated for 5-s during reinforcement and a 5-s dark intertrial interval (ITI) followed. If more than five responses were made, however, the houselight immediately extinguished and a 10-s dark ITI began as an analogy to the balloon popping (see Table 2.1). Each session consisted of 60 trials. Training continued for 24 sessions, after which forced choice trials were added to encourage additional pecking to the add key prior to cashing out. Forced choice trials were identical to free choice trials except that there was no risk of the balloon popping and the cash out key only delivered reinforcement when a randomly chosen minimum number of responses (between 2 and 5) to the add key had been made. Each

session consisted of 20 forced choice and 40 free choice trials, and the phase continued for 40 sessions.

Discrimination Training. Prior to the assessment of delay discounting, the pigeons were tested for their ability to discriminate between the smaller and larger magnitudes of reinforcement. Pigeons were first given six sessions of habituation pre-training to responding to novel stimuli (FR1) while the house light was off. The novel stimuli included a center white line on a dark background and two red side keys. As opposed to the BELT task, the houselight was only illuminated for 5-s during reinforcement, followed by a 5-s dark ITI.

Discrimination training then followed which was modeled after Laude, Beckmann, et al. (2014) and Evenden and Ryan (1996). Each session consisted of five seven-trial blocks, the first two of which were always forced choice trials and the last five were always free choice trials for a total of 35 trials. Forced choice trials began with an orienting response to the white line on the center key, after which either the left or right red stimulus randomly appeared, each spatially associated with either the SS reward (1 pellet) or the LL reward (4 pellets). Once a response was made, the house light illuminated for 5-s, reinforcement was delivered, and the house light extinguished again for 5-s prior to the next trial for a 10-s ITI. Free choice trials were identical to forced choice except that, following the orienting stimulus, both the left and right red stimuli appeared, allowing the subject to choose between the stimulus associated with one versus four pellets. The pigeons continued on this task until they chose the four pellet alternative at least 80% of the time for three consecutive sessions.

Delay Discounting Task. The delay discounting task was identical to the discrimination training except that delays were inserted for the stimulus associated with the LL alternative. The delays ascended across within-session blocks in order of 0, 2.5, 5, 10,

and 20 s. If the LL was chosen, the alternative SS stimulus immediately extinguished and the delay began, after which the LL stimulus extinguished and reinforcement was delivered on a fixed time (FT) schedule as previously described. The ITI was also increased from a 5-s lit and 5-s dark ITI to a 5-s lit and variable dark ITI that fixed the total durations between trials 30 s so that choosing the SS alternative did not result in the next trial occurring sooner. The delay discounting task lasted for a total of 30 sessions.

Suboptimal Choice Task. The pigeons were then moved directly to the suboptimal choice task (Stagner & Zentall, 2010; Zentall, 2011). This task consisted of both free and forced choice trials of a low-probability, high-magnitude reward and a high-probability, low-magnitude reward. On free choice trials, trial onset began with a white center orienting stimulus. Pecks offset the center stimulus and was followed by a choice between two white stimuli, one on the left and one on the right. As illustrated in Figure 1, for all pigeons, choosing the left side resulted in either a red stimulus 20% of the time or a blue stimulus 80% of the time. Choosing the right side resulted in either a green stimulus 20% of the time or a yellow stimulus 80% of the time. Both the green and red stimuli, which had previous reinforcement history, were counterbalanced as the low probability stimulus on each choice alternative.

The suboptimal side was then assigned to the previous LL key from the delay discounting task. If the suboptimal alternative was chosen and the low probability stimulus appeared, 10 pellets of food was delivered after 10 s on a fixed interval (FI) schedule. As in the delay discounting task and discrimination training, the houselight illuminated for 5 s during reinforcement and then extinguished for 5 s. Alternatively, if the high probability stimulus appeared, it remained on for 10 s on a FT schedule, after which it extinguished and

a 10 s dark ITI ensued. If the optimal alternative was chosen, both stimuli predicted 3 pellets of food 100% of the time, with only the frequency of stimulus appearance differing. Thus, choice of the suboptimal alternative averaged 2 pellets of food per trial, while choice of the optimal alternative averaged 3 pellets of food. Forced choice trials were identical to free choice except that, following a response to the orienting stimulus, only one of the side keys would illuminate, forcing the pigeon to experience that option. The task consisted of a total of 40 forced choice trials and 20 free choice trials and lasted a total of 12 sessions.

Data Analysis. Four primary variables were used to quantify the BELT task over the last 10 sessions taken from the literature: BELT pecks per trial (BELTppt), or the average number of pecks to the add key across trials, BELT adjusted pecks per trial (BELTAdjppt), or the average number of pecks to the add key only on win trials that preceded a successful cash out, BELT pellets earned (BELTPellets), or the average number of food pellets earned, and BELT Losses (BELTLoss), or the average number of loss trials in which the pigeon pecked the add key six times. Additionally, effects of the previous outcome were assessed by calculating the average number of pecks made following wins and losses.

For the delay discounting task, the primary variable of interest was the number of LL choices made across the session at the varying LL delays. From this measure, k values were modeled using Equation 1:

$$V = \frac{A}{(1 + k D)}$$

where V is the subjective value of the reward, A is the amount of the reward, D is the delay to the reward, and k is a free parameter fitting the slope of line, indicating the individual's rate of discounting (Odum, 2011; Reed, Kaplan, & Brewer, 2012; Reynolds, 2006). Here, higher k values indicate steeper discounting and greater impulsivity. In addition, area under the

curve (AUC) measurements were also calculated to gain a theoretically neutral metric of delay discounting (Myerson, Green, & Warusawitharana, 2001; Reed et al., 2012) by normalizing the data and calculating the area below the curve between each data point using Equation 2:

$$(x_2 - x_1)[(y_1 + y_2)/2]$$

where x_1 and x_2 are delays to the LL alternative, and y_1 and y_2 are percent LL choice at delay x . For this measure, steeper discounting is associated with lower AUC values and is inversely related to k -values.

Finally, the primary variable in the suboptimal choice task was the number of sessions to gambling acquisition due to a high ceiling effect in which all pigeon showed the same asymptotic level of preference. A criterion of choosing the suboptimal alternative 95% of the time (19/20 trials) over two consecutive sessions was defined as having acquired a preference for the suboptimal alternative.

All statistics and model fits were calculated using SPSS and GraphPad Prism software. In order to correct for normality, statistics were run with a square root transform where appropriate with the primary variables' descriptive statistics shown in Table 2.2.

Results

BELT. Illustrated as raw values in Figure 2.2 (top), the pigeons in the BELT task pecked well below the optimal five times prior to cashing out across acquisition and in the final 10 sessions of training ($M = 2.53$, $SEM = 0.21$), although there were individual differences. The dotted line indicates the addition of forced choice trials, which appeared to slightly increase the average pecks per trial. To quantify this, a paired samples t-test was run between the transformed average number of pecks made on the last 10 session prior to

adding forced choice trials ($M = 1.36$, $SEM = 0.07$) and the last 10 sessions of training with forced choice trials ($M = 1.57$, $SEM = 0.07$). The results indicated a significant increase following the addition of forced choice trials, $t(9) = 3.64$, $p = .005$, $d = 1.17$, as well as a significant correlation, $r = .67$, $p = .035$, indicating the rank order of individuals stayed relatively stable. Also shown in Figure 2.2 (middle) is the frequency of peck trial types, or the frequency with which a number of pecks (i.e., 1-6) was made during the last 10 sessions of training. As can be seen, the pigeons continued to peck only a few times and distributed the number of pecks made most frequently between 1 and 3 times. 1 was the modal peck frequency occurring around 30% of the time ($M = .29$, $SEM = 0.06$) although again there were individual differences. These differences are illustrated more clearly in the bottom panel of Figure 2.2 which shows the varying levels of total food pellets earned over the last 10 sessions of training in relation to the pigeons' average BELT pecks per trial. In general, pigeons that pecked more on average tended to earn greater food rewards.

In order to quantify the nature of these individual differences, Pearson bivariate correlations were run on each of the primary transformed BELT variables. Shown in Table 2.3 and illustrated in Figure 2.3, each metric was significantly and positively related to each other. In general, pigeons that pecked more often cashed out at higher values, experiencing a greater number of losses, and earned more pellets per session. Finally, to get a measure of more local behavioral differences and the potential effects of a loss, the average pecks following a win ($M = 2.57$, $SEM = 0.20$) versus a loss ($M = 2.67$, $SEM = .32$) were calculated. One pigeon had to be omitted due to never experiencing a loss in the last 10 sessions. The results showed no statistical difference following either outcome, $t(8) = -0.41$,

$p = .695$, $d = -0.16$, but a significant correlation, $r = .71$, $p = .034$, indicating that losing seems to have little effect on the pigeons' behavior.

Discrimination Training. All pigeons discriminated between one and four pellets of food reliably for three consecutive sessions (M sessions to criterion = 4.2, $SEM = .533$).

Delay Discounting Task. Illustrated in Figure 2.4, the pigeons reliably chose 4 pellets over 1 at zero delay (identical to discrimination training); however, preference quickly switched to preferring the SS alternative at even the shortest delay of 2.5 s ($M = 44.60$, $SEM = 7.76$). At 5 s and beyond, the pigeons chose the SS almost exclusively. Table 2.4 shows the parameter estimates for both k ($M = 1.50$, $SEM = 0.41$) and AUC ($M = .15$, $SEM = 0.03$) values which were inversely correlated with each other, $r = -.82$, $p = .003$. Model fits estimating k values using equation 1 described the data well ($M r^2 = .92$, $SEM = 0.02$); Figure 2.5 shows two example fits.

Suboptimal Choice Task. Illustrated in Figure 2.6 and consistent with previous research (Laude, Beckmann, et al., 2014; Stagner & Zentall, 2010), the pigeons began choosing optimally (preferring the optimal alternative), but quickly switched to preferring the suboptimal alternative. Given the high ceiling effect of preference, acquisition to a criterion of 95% suboptimal preference over two consecutive sessions, rather than steady-state performance, was used as a measure of individual differences. The criterion was quickly met by all birds, ($M = 8.2$, $SEM = 0.76$) but with individual differences in their acquisition of this preference.

Between task associations. To assess interrelationships among tasks, Table 2.2 further shows Pearson correlations that were run between the primary variables of each task. The results showed no relationships between the delay discounting task and BELT or

suboptimal choice tasks. All four metrics from the BELT task, however, inversely correlated with acquisition of the suboptimal choice task (see Figure 2.7). These results indicated that increased pecks per trial, cashing out after a larger number of pecks, greater pellets earned, and more frequent losses in the BELT task were all associated with faster acquisition of the suboptimal gambling task.

Given the strong previous research linking the suboptimal choice and delay discounting tasks (Laude, Beckmann, et al., 2014), it was surprising to find no association in the present sample with either k or AUC values. While the present sample did not support a simple relationship between delay discounting and suboptimal choice task, the possibility remains of an additive or interaction model between the BELT and delay discounting in predicting suboptimal choice. As such, three multiple regression models testing for interaction effects with each of the primary metrics from the BELT task and delay discounting k and AUC values were run. As there was no strong theoretical reason for either variable to enter into the model first, the variable accounting for the most variance (BELT variables in all cases) was entered first followed by the delay discounting variable and finally the interaction term. All predictors were mean centered in order to reduce the effects of multicollinearity.

Models including delay discounting k values are shown in Tables 2.5-8. For all models, the addition of delay discounting k values did not significantly add to the variance explained. Adding the interaction term in the third step, however, explained a significant amount of variance in the BELT adjusted pecks per trial, $F_{change}(1, 6) = 6.00, p = .05$, and BELT pellets earned, $F_{change}(1, 6) = 6.47, p = .044$, models. For the BELT adjusted pecks model, BELT adjusted pecks, $t = -4.07, p = .007$, and the interaction term, $t = -2.45, p = .050$,

were significant predictors in the overall model, $F(3, 6) = 8.15, p = .015$. For the BELT pellets model, BELT pellets, $t = -3.68, p = .01$, and the interaction term, $t = -2.45, p = .044$, were significant in the overall model, $F(3, 6) = 6.86, p = .023$. The interaction term for the BELT pecks per trial model fell just outside of significance, $p = .071$.

Models using delay discounting AUC values are shown in Tables 2.9-12. Similar to the k values, adding AUC values as the second step to the model did not contribute to greater variances explained. The addition of the interaction term, however, explained a significant amount of variance in the BELT losses model, $Fchange(1, 6) = 6.56, p = .043$. In this model, both BELT losses, $t = -3.24, p = .018$, and the interaction term, $t = 2.56, p = .043$, were significant predictors in the overall model, $F(3, 6) = 6.72, p = .024$. The interaction terms for the BELT adjusted pecks, $p = .051$, and BELT pecks per trial, $p = .075$, models fell just outside of significance.

The three significant interaction models are illustrated in Figure 2.8. In the left column the primary BELT variable is plotted as a function of the suboptimal choice acquisition on the left y-axis and the delay discounting moderating variable on the right y-axis. The right column shows the predicted results based on the mean centered regression coefficients of each model using the mean \pm one SD to plot the functions. As can be seen in the BELT adjusted pecks and BELT pellets earned models, high k values, indicative of greater discounting, had the steepest association with suboptimal choice acquisition, while low k values had a much flatter slope. These slopes indicate that, when k values are high, acquisition of suboptimal choice will be slow when BELT adjusted pecks and BELT pellets are also low, but faster when both variables are high. For the BELT losses model, low AUC values, indicative of greater discounting, appeared to have a similar slope as mean and low

AUC values, but the line was shifted above the others, indicative of slower suboptimal acquisition when the greater the level of discounting without crossing as in the previous two models.

Discussion

The present study sought to assess the validity of a pigeon model of risk taking using the BELT, a variant of the BART with a fixed explosion point, a delay discounting task to measure impulsivity, and the suboptimal choice task to measure analogous gambling behavior. The results showed that the pigeons, as a group, only pecked an average of 2.5 times prior to cashing out but with individual differences. The pigeons also showed a large degree of impulsivity, choosing the SS almost exclusively when the delay to the LL was only 5 s, and all quickly acquired a suboptimal preference in the suboptimal choice task. Additionally, all primary variables of the BELT task were interrelated and showed inverse correlations with suboptimal choice acquisition, indicating that greater pecks per trial tended to be associated with greater pecks prior to cashing out, experiencing more losses, and earning more pellets along with faster acquisition of the suboptimal gambling task. Delay discounting measures also showed evidence of moderating the relationship between BELT adjusted pecks per trial, BELT pellets, and BELT losses when predicting suboptimal choice acquisition. Together, these results support the hypothesis that BELT risk taking is associated with suboptimal choice risk taking and are weakly moderated by delay discounting impulsivity values.

BELT. Like both rats (Jentsch et al., 2010) and humans (Lejuez et al., 2002), the pigeons in the present experiment showed suboptimal performance, pecking the add key less than what would maximize reward within a trial or session. Adding forced choice trials

significantly increased the amount of pecking, but only slightly. These results with the BELT differ from the others using the BART, though, in that losses only occurred after 5 pecks and were relatively infrequent, making the reason for the suboptimal add key pecking likely different. Some pigeons always pecked only once or twice followed by cashing out, exploiting the low pump choices and rarely experiencing losses, while others pumped more regularly and variably, showing greater exploration behaviors and experiencing greater losses. Despite these characteristics, delay discounting impulsivity levels also showed no relation to the amount of BELT pecks, possibly suggesting that the delay of gratification in this task may not play a role. However, this may be because the relative number of pecks was low, restricting the possibility of assessing this finding. Alternatively, it may be that other factors, such as motor inhibition to the cash out key, may exert more control in this task rather than delay of gratification (see Evenden, 1999).

In fact, over the last 10 sessions of the BELT, less than 10% of free choice trials were ever losses. Additionally, the number of pecks following losses was no different than following wins. This may suggest that pigeons are indeed insensitive to the losses in the BELT task similar to what has been shown in the suboptimal choice task (Laude, Stagner, et al., 2014; Zentall, 2011) and problem gamblers (van Holst et al., 2010). Alternatively, the present results may also stem from differences in the way that early losses affect the pigeons. Early losses in training may decrease responding to the add key to only a few times prior to cashing out for some birds, show insensitivity to losses within a session after training but not necessary losses altogether. This might suggest some pigeons show sensitivity to losses early on but reducing their number of pecks while others continue to peck in high numbers despite the losses.

While the discrimination between winning and losing (immediate house light offset) is presumably discriminable, the lack of optimal add key pecks may also be attributable to a lack of discriminability. This BELT task employed a spatial discrimination similar to previous studies using rats (Ashenurst et al., 2012; Jentsch et al., 2010), but pigeons may have difficulty discriminating the linear increase in the number of pellets or responses. Many studies of non-human animals' perception suggest a logarithmic account such as Weber's law or a power function (see Stevens, 1957 for a discussion) and rely on a proportional 2:1 ratio difference as a shorthand for reliable discrimination. The present research employed a linear scale similar to the original balloon task even though this may be less applicable for animal analogues. Previous research has shown, however, that pigeons may be capable of tracking up to four biologically relevant events (Rayburn-Reeves, Miller, & Zentall, 2010), although this research is different in that the fourth event was nonreinforcement whereas the first three were reinforcement. The present experiment was notably different in that it delivered up to five reinforcements in rapid succession. Thus, it may be difficult for the pigeons to discriminate either/both the number of pecks made or the outcome of number of pellets on a given trial.

Delay Discounting and Suboptimal Choice. The pigeons in the present task showed similar behavior in both the delay discounting task (Laude, Beckmann, et al., 2014) and suboptimal choice task (Stagner & Zentall, 2010; Zentall, 2011) as previous experiments. The magnitude of the behavior, however, was greater in the present experiment. In the delay discounting task the pigeons preferred the SS when even a small delay (2.5 s) was added to the LL reward, further preferring the SS almost exclusively with a 5 s LL delay. The pigeons in the suboptimal choice task also acquired the suboptimal preference relatively quicker and

at a greater asymptotic level than previous reports (Laude, Beckmann, et al., 2014). This difference, however, may be explained by the use of a spatial versus visual discrimination, as previous reports using spatial discriminations have shown generally faster learning (e.g. Stagner & Zentall, 2010) similar to the present experiment.

Between Task Correlations. In the current experiment, all primary variables of the BELT task correlated, indicating that greater pecks to the add key were associated with greater pecks prior to cashing out, number of experienced losses, and total pellets earned. Thus, it is sufficient to say in this task that greater amounts of pecking resulted in the optimal behavior.

Additionally, all of the BELT variables inversely correlated with suboptimal preference acquisition, indicating that the greater amounts of pecking and by extension losses. This implies that greater amounts of risk taking in the BELT task, which was an adaptive risk taking behavior, was associated with a separate maladaptive risky behavior, similar to human experiments (e.g. Fernie et al., 2010; Hopko et al., 2006; Skeel et al., 2007). There are multiple interpretations these data could take on. One interpretation of these results may be that different associative sensitivity to the reinforcement magnitudes resulted in greater pecks on the balloon task. Indeed, this could also correlate with suboptimal choice acquisition as recent research from our lab has shown that the suboptimal choice task seems to largely depend on the value of the conditioned reinforcers (Smith & Zentall, under review; Zentall et al., 2015). As such, greater discriminability of the conditioned reinforcers may an underlying mechanism with the current version of the BELT task and acquisition of the suboptimal choice task.

It was surprising to find, however, no correlation between delay discounting variables and either the BELT or suboptimal choice tasks. The latter was surprising because of previous reports of significant associations between delay discounting and the suboptimal choice task in pigeons (Laude, Beckmann, et al., 2014) as well as other risk tasks in rats (Kirkpatrick, Marshall, Smith, Koci, & Park, 2014). However, important differences between the studies exist. For example, the Laude, Beckmann, et al. (2014) used a visual discrimination for the suboptimal choice task, appearing to both slow choice acquisition and correlated delay discounting with asymptotic preference levels that were qualitatively lower than the present experiment. Additionally, that experiment also used an environmental enrichment manipulation that was collapsed over, whereas the present study had no such manipulation. Thus, the differences seem sufficient enough to possibly implicate other underlying mechanisms.

Despite the lack of a simple association between delay discounting and the BELT task, multiple regression models did support a modulating interaction between the BELT and delay discounting tasks when predicting the suboptimal choice task. Both BELT adjusted pecks and BELT pellets earned showed a disordinal interaction with delay discounting k values such that high discounting was associated with slow acquisition when BELT adjusted pecks were low (or BELT pellets), but fast acquisition when they were high. Conversely, low discounting was associated with a relatively flat slope indicative of discounting levels having little effect on the relationship between the BELT and suboptimal choice tasks. This may suggest that discounting in the BELT task may either increase decrease adjusted pecks (and subsequently, pellets earned). The latter may be due to focusing on the lower order

conditioned reinforcer of the cash out key (relative to the add key), or increase them similar to the human experiments.

AUC values showed a similar modulation effect but only with BELT losses. Low AUC values relative to high were associated with overall slower suboptimal choice acquisition; however, average AUC values were associated with slower acquisition in conjunction with high BELT losses. While there was no a priori reason for why these two measures should not corroborate each other, one possibility might be that because AUC values adjust for different y-intercepts (unlike k values with a fixed y-intercept), AUC values may have only modulated with losses by taking into account these different y-intercepts. Thus, if choosing 1 pellet over 4 in the DD task can be seen as indiscriminate pecking, AUC values may have had greater power to detect possibly similar indiscriminate pecking in the BELT task of going over five pecks.

Experiment 1 supported some of the predicted hypothesis in that the BELT task was related to the suboptimal choice task and possibly modulated by delay discounting levels. However, the interpretation of Experiment 1 is also less clear due to the low number of BELT pecks made and their relative inexperience with the loss contingency. As such, Experiment 2 attempted to replicate the present findings but also improving the number of pecks made, making it possible to assess the actual BART task.

Table 2.1. Design parameters for the BELT task. *Note:* the bolded column indicates the optimal point of responding to maximize reinforcement per trial.

Add Key Responses	1	2	3	4	5	6
p(Win)	100%	100%	100%	100%	100%	0%
Expected Value	1	2	3	4	5	0

Table 2.2. Descriptive statistics for the primary variables in Experiment 1 both before and after a square root transform was applied. Normality was assessed according to a Shapiro-Wilks test.

	Raw Scores Mean (95% CI)	Normality <i>p</i> -value (n)	Square Root Mean (95% CI)	Normality <i>p</i> -value (n)
BELT Pecks per Trial	2.64 (2.14-3.14)	.022 (100)	1.61 (1.45-1.76)	.706 (100)
BELT Adjusted Pecks per Trial	2.49 (2.06-2.91)	.035 (100)	1.56 (1.43-1.70)	.881 (100)
BELT Pellets	93.52 (79.89-107.16)	.239 (100)	—	—
BELT Losses	2 (.62-3.38)	< .001 (100)	1.04 (.50-1.58)	.404 (100)
Delay Discounting <i>k</i>	1.59 (.52-2.67)	.023 (10)	1.16 (.75-1.57)	.279 (10)
Delay Discounting AUC	0.15 (.08-.21)	.012 (10)	0.37 (.29-.45)	.094 (10)
Suboptimal Choice Criterion	8.11 (6.06-10.16)	.609 (10)	—	—

Table 2.3. Pearson Correlation matrix between the primary metrics of the BELT, delay discounting, and suboptimal choice tasks.

	1	2	3	4	5	6	7
Sqrt BELT Pecks per Trial ¹	—						
Sqrt BELT Adjusted Pecks per Trial ²	.99***	—					
BELT Pellets ³	.96***	.99***	—				
Sqrt BELT Losses ⁴	.93**	.89***	.81**	—			
Sqrt Delay Discounting k values ⁵	-.28	-.30	-.34	-.14	—		
Sqrt Delay Discounting AUC ⁶	.44	.49	.56	.26	-.82**	—	
Sub-optimal Choice Criterion ⁷	-.74*	-.73*	-.68*	-.70*	.49	-.36	—

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 2.4. Parameter estimates for both Delay Discounting k and area under the curve values.

Bird	DDk	SqrtDDk	r^2	DDauc	SqrtDDauc
20	0.9664	0.983056	0.8973	0.1237	0.1237
710	4.2064	2.050951	0.995	0.0775	0.0775
713	1.1803	1.086416	0.9419	0.1196	0.1196
720	1.5675	1.251998	0.9625	0.1008	0.1008
721	0.6141	0.783645	0.8879	0.1563	0.1563
723	0.6498	0.806102	0.9063	0.1607	0.1607
1056	0.2704	0.520000	0.957	0.3581	0.3581
19227	3.5759	1.891005	0.9751	0.0819	0.0819
19229	0.3245	0.569649	0.7499	0.2213	0.2213
19836	1.6132	1.270118	0.9697	0.1029	0.1029

Table 2.5. Regression interaction model of BELT pecks per trial and delay discounting k values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.49*	–
SqrtBELTppt	-8.32*	-14.49 – -2.14	.55	–	–
Step II:	–	–	–	.53*	.04
SqrtBELTppt	-7.37*	-13.72 – -1.02	.40	–	–
SqrtDDk	1.49	-1.29 – 4.26	.08	–	–
Step III:	–	–	–	.69*	.16
SqrtBELTppt	-9.34**	-15.08 – -3.61	.54	–	–
SqrtDDk	1.11	-1.24 – 3.45	.05	–	–
BELTppt*DDk	-12.24	-25.93 – 1.45	.16	–	–

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 2.6. Regression interaction model of BELT adjusted pecks per trial and delay discounting k values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.47*	–
SqrtBELTAdjppt	-9.35*	-16.55 – -2.14	.53	–	–
Step II:	–	–	–	.49*	.02
SqrtBELTAdjppt	-8.21*	-15.78 – -0.64	.37	–	–
SqrtDDk	1.44	-1.45 – 4.32	.08	–	–
Step III:	–	–	–	.70*	.21*
SqrtBELTppt	10.92**	-17.49 – -4.36	.54	–	–
SqrtDDk	1.05	-1.26 – 3.63	.04	–	–
BELTAdjppt*DDk	-14.76*	-29.51 – -0.02	.20	–	–

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 2.7. Regression interaction model of BELT pellets earned and delay discounting k values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.39*	–
BELTPellets	-0.09*	-0.17 – -0.01	.46	–	–
Step II:	–	–	–	.40	.01
BELTPellets	-0.08	-0.16 – 0.01	.29	–	–
SqrtDDk	1.43	-1.76 – 4.62	.08	–	–
Step III:	–	–	–	.66*	.26*
BELTPellets	-0.11**	-0.19 – -0.04	.51	–	–
SqrtDDk	1.06	-1.44 – 3.55	.04	–	–
BELTPellets*DDk	-0.16*	-0.31 – -0.01	.24	–	–

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 2.8. Regression interaction model of BELT losses and delay discounting k values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.42*	–
SqrtBELTLosses	-2.39*	-4.38 – -0.39	.49	–	–
Step II:	–	–	–	.54*	.12
SqrtBELTLosses	-2.19*	-4.05 – -0.34	.40	–	–
SqrtDDk	-1.93	-0.73 – 4.59	.15	–	–
Step III:	–	–	–	.51	-.03
SqrtBELTLosses	-2.39*	-4.45 – -0.33	.44	–	–
SqrtDDk	1.77	-1.09 – 4.64	.12	–	–
BELTLosses*DDk	-2.06	-8.38 – 4.26	.03	–	–

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 2.9. Interaction model of BELT pecks per trial and delay discounting AUC values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.49*	–
SqrtBELTppt	-8.32*	-14.49 – -2.14	.55	–	–
Step II:	–	–	–	.42	-.05
SqrtBELTppt	-8.13*	-15.66 – -0.60	.42	–	–
SqrtDDauc	-0.96	-18.39 – 16.48	.00	–	–
Step III:	–	–	–	.62	.20
SqrtBELTppt	-8.14*	-14.46 – -1.81	.42	–	–
SqrtDDk	0.28	-14.44 – 15.00	.00	–	–
BELTppt*DDauc	3.83	-0.53 – 8.19	.20	–	–

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 2.10. Interaction model of BELT adjusted pecks per trial and delay discounting AUC values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.47*	–
SqrtBELTAdjppt	-9.35*	-16.55 – -2.14	.53	–	–
Step II:	–	–	–	.39	-.08
SqrtBELTAdjppt	-9.32*	-18.35 – -0.28	.40	–	–
SqrtDDauc	-0.12	-18.40 – 18.17	.00	–	–
Step III:	–	–	–	.50	.11
SqrtBELTppt	-5.80	-15.83 – 4.23	.11	–	–
SqrtDdauc	10.32	-13.12 – 33.76	.06	–	–
BELTAdjppt*DDauc	-27.56	-69.83 – 14.70	.14	–	–

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 2.11. Interaction model of BELT pellets earned and delay discounting AUC values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.39*	–
SqrtBELTPellets	-0.09*	-0.17 – -0.01	.46	–	–
Step II:	–	–	–	.30	-.09
SqrtBELTPellets	-0.09	-0.16 – 0.01	.33	–	–
SqrtDDauc	0.92	-19.85 – 21.69	.00	–	–
Step III:	–	–	–	.40	.10
SqrtBELTPellets	-0.11*	-0.22 – -0.01	.45	–	–
SqrtDDauc	0.04	-20.01 – 20.10	.00	–	–
BELTPellets*DDauc	-19.96	-53.80 – 13.88	.14	–	–

* $p < .05$, ** $p < .01$, *** $p < .001$

Table 2.12. Interaction model of BELT Losses and delay discounting AUC values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.42*	–
SqrtBELTLosses	-2.39*	-4.38 – -0.39	.49	–	–
Step II:	–	–	–	.38	-.04
SqrtBELTLosses	-2.22*	-4.41 – -0.03	.39	–	–
SqrtDDauc	-4.83	-21.55 – 11.88	.03	–	–
Step III:	–	–	–	.66*	.28*
SqrtBELTLosses	-2.43*	-3.94 – -0.55	.40	–	–
SqrtDDauc	-3.00	-16.03 – 10.03	.01	–	–
BELTLosses*DDauc	0.87*	0.04 – 1.70	.25	–	–

* $p < .05$, ** $p < .01$, *** $p < .001$

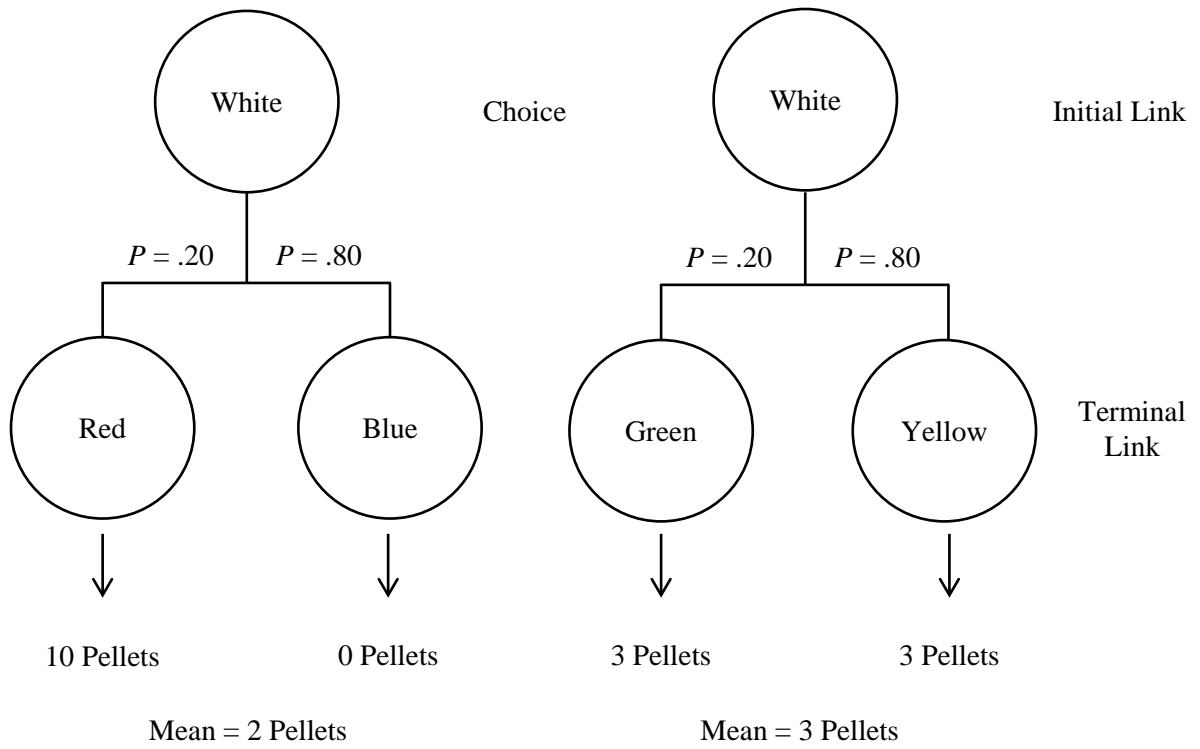


Figure 2.1. Design of the suboptimal choice task in Experiment 1. The location of the suboptimal alternative was counterbalanced across subjects.

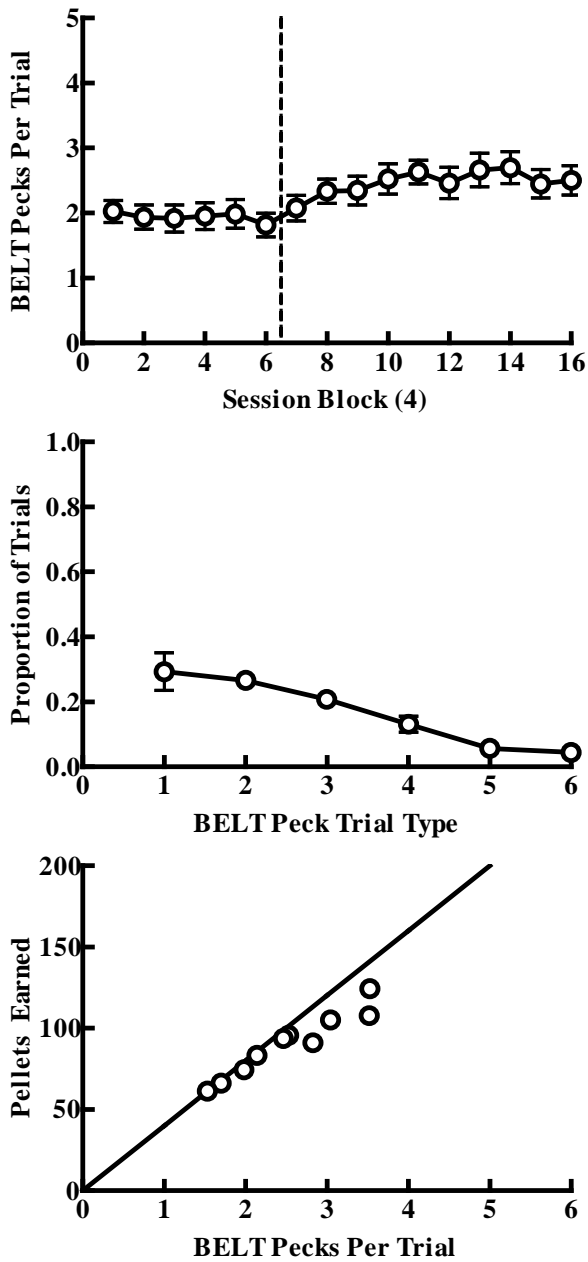


Figure 2.2. Top. Mean (\pm SEM) BELT pecks per trial across acquisition. The dotted line indicates the point at which forced choice trials were introduced. Middle. Mean (\pm SEM) peck trial type frequency averaged over the last 10 sessions. Bottom. Total pellets earned as a function of pigeons' average BELT pecks per trial over the last 10 sessions where the black line indicates total possible reinforcements.

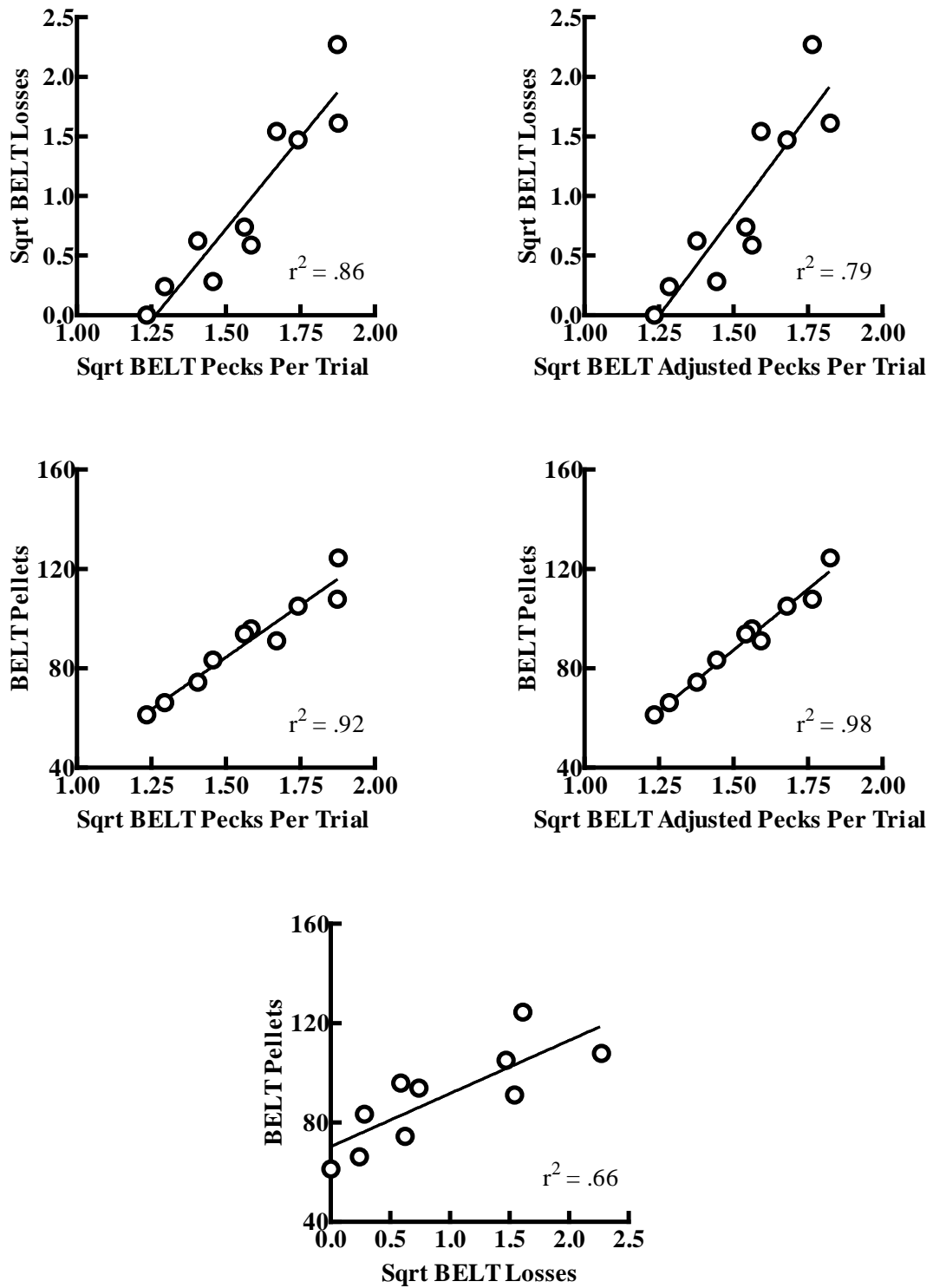


Figure 2.3. Significant Pearson correlations between the primary BELT variables.

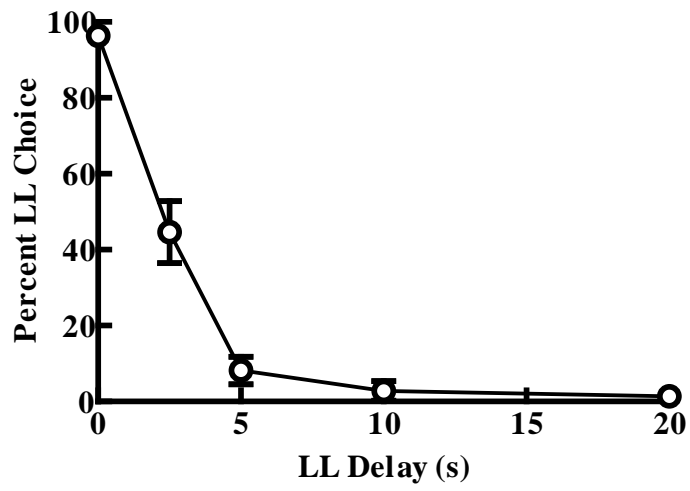


Figure 2.4. Mean (\pm SEM) percent LL choice over the last 10 sessions of training.

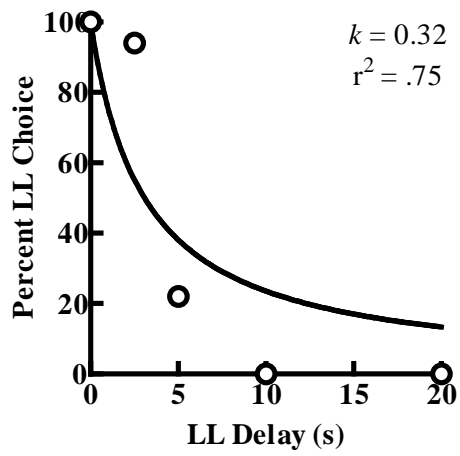
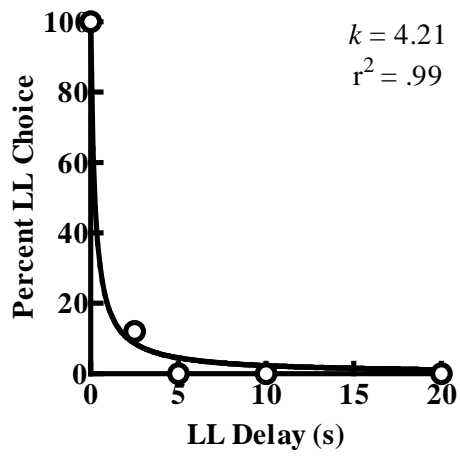


Figure 2.5. Example k parameter fits using equation 1 for birds 710 (top) and 19229 (bottom).

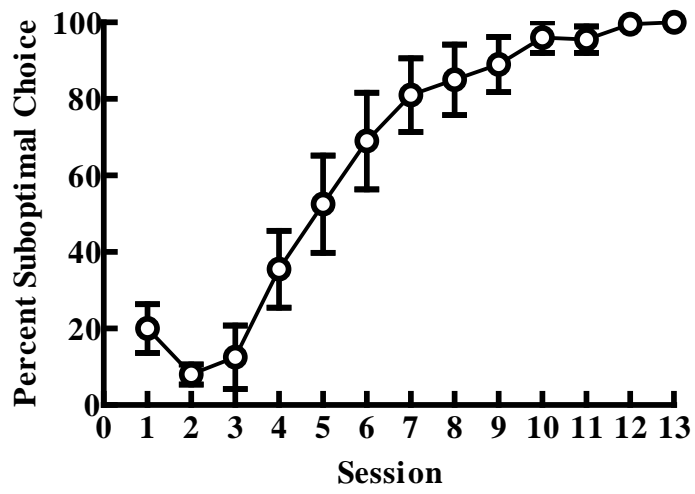


Figure 2.6. Mean (\pm SEM) percent choice of the suboptimal alternative across the 13 sessions of training.

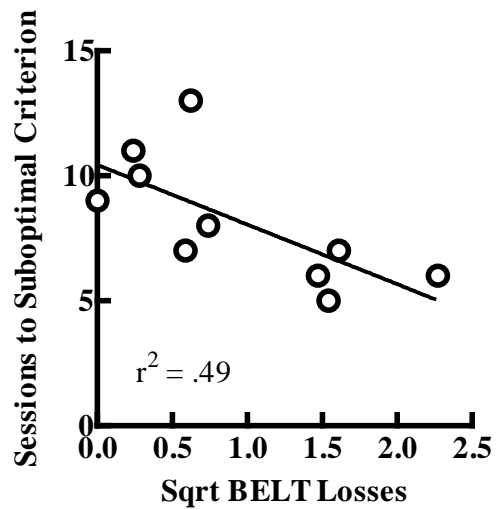
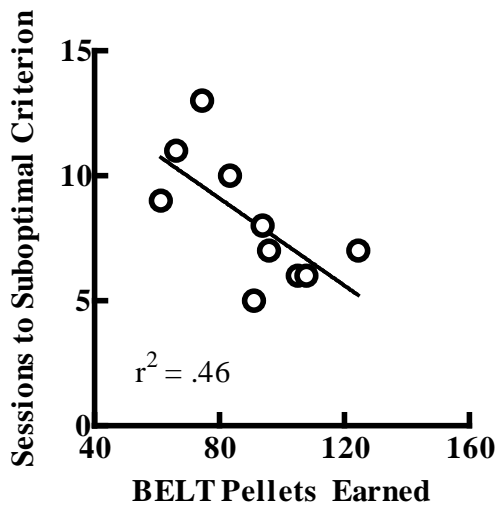
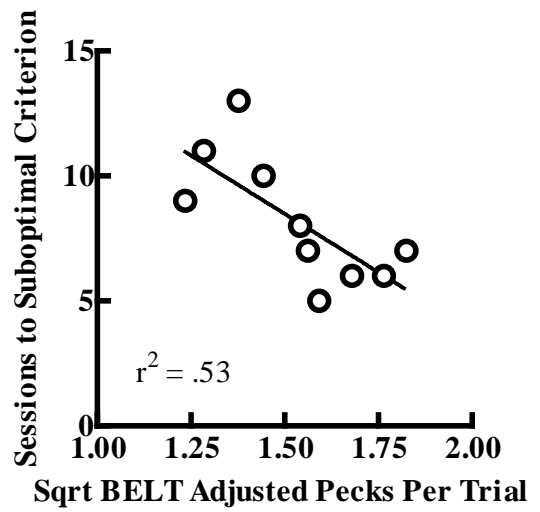
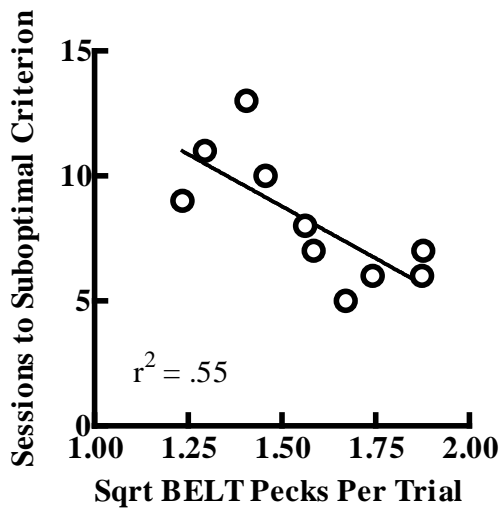


Figure 2.7. Significant correlations between the BELT and suboptimal choice primary variables.

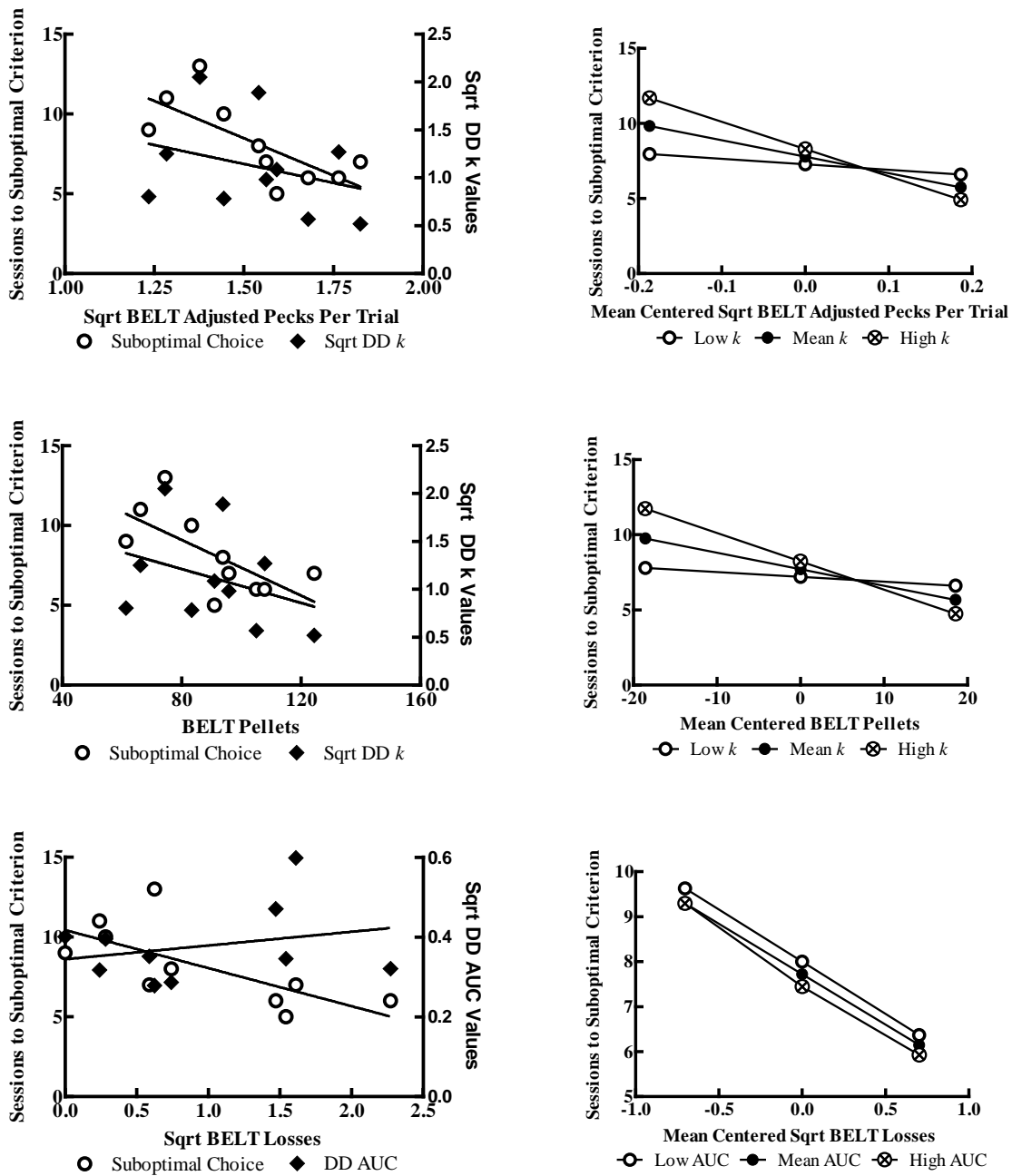


Figure 2.8. Left Column. Interaction effects of suboptimal choice acquisition and delay discounting k values as a function of Sqrt BELT adjusted pecks per trial (top) and BELT pellets earned (middle) and suboptimal choice acquisition and delay discounting AUC values as a function of Sqrt BELT losses (bottom). **Right Column.** Predicted values of suboptimal choice acquisition as a function of mean centered Sqrt BELT adjusted pecks per trial at low, medium, and high delay discounting k values (top), as a function of mean centered BELT pellets at low, medium, and high delay discounting k values (middle), and as a function of mean centered Sqrt BELT losses at low, medium, and high delay discounting AUC values (bottom).

Section 3: Experiment 2

One hypothesis of why the BELT pecks in Experiment 1 were low was due to poor discriminability of pecks made and / or choice outcomes. Thus, in order to increase this discriminability in Experiment 2, each peck was signaled by a different color that changed with each add key peck, signaling both number of pecks and the expected reward. To increase the discriminability of the number of reinforcers, a separate, possibly more salient form of reward delivery using number of hopper accesses was tested. Using a hopper requires raising it to a darkened magazine that is then illuminated, utilizing both a salient visual and auditory stimulus in that it makes a relatively louder sound than the pellet dispenser. Finally, Experiment 2 also employed shorter delays in the discounting task in order to reduce the floor effect found in Experiment 1.

Method

Animals. 20 experimentally non-naïve White Carneau pigeons were used in the experiment with all aspects of their housing identical to Experiment 1. All of the animals had prior experience with suboptimal choice tasks but not delay discounting, BELT, or BART tasks.

Apparatus. The experiment was conducted in two Med Associates (St. Albans, VT) modular operant chambers, one of which was the same chamber as Experiment 1. The second chamber was similar but measured $36 \times 36 \times 36$ cm and responded to three keys similar to that described in Experiment 1. The primary difference between the two chambers was a center-mounted feeder was located 10 cm above the floor which, when raised, was illuminated by a 28-V 0.04-A lamp that allowed access to mixed grain.

Procedure

Pretraining. For subjects in the pellet group, two sessions of habituation training followed by magazine training were conducted similar to Experiment 1. For subjects in the hopper group, the experiment began with multiple hopper training in which hoppers of varying numbers (1-5) occurred on a VT 30-s schedule similar to Experiment 1 and the pellet group followed by a 10-s ITI. Sessions started with the illumination of the house light and each hopper being raised with the onset of the hopper light for 1.5 s, lowered for 1 s with hopper light offset, and then raised again until the appropriate number of hoppers had been delivered. Once all of the hoppers had been delivered, both the hopper and house lights offset. After two sessions in which it was observed that the pigeon was able to consume at least one peck of food at every raised hopper for five consecutive trials, the hopper duration was shortened to 1.25 s until the same criterion was met to reduce the amount of food obtained in a session.

Once consistent magazine training was obtained in both groups, auto shaping procedures with a white center stimulus appeared for 30 s. Following the delay elapsing or a peck to the stimulus, the appropriate reinforcement occurred followed by a 10 s ITI. For the hopper group, the hopper duration was shortened to 1 s with a .2 s delay between either a peck to or offset of the stimulus to ensure the pigeon could reach the first hopper. Following two sessions in which the pigeon pecked the stimulus on all trials, a similar auto shaping procedure to a white right stimulus was used. This same criterion was used for the remainder of training sessions. The pigeons were then trained in which both a white center and right stimulus appeared. One peck was required first to the right stimulus, changing both stimuli to either yellow or green, counterbalanced across birds. A peck to the cash out key then delivered one reinforcer. After training criterion had been met, pecks to the right key were

increased by 1 up to an FR5 across sessions while pecks to the center key remained at 1. Each peck to the right key changed the color of both keys in order of yellow, red, purple, blue, and green for half the pigeons (reversed for the other half) depending on which FR the training session was currently on. Pecks made greater than the FR to the right key had no consequence. After completing the FR to the right key, a single peck to the center key produced the same number of reinforcers as the FR on the right key. Total training lasted approximately 60 sessions.

BELT. The pigeons then moved to the BELT task. The contingencies and procedure were identical to Experiment 1 (see Table 2.1) except the colors of the add and cash out key changed with each peck in the manner described above. Additionally, due to the different reinforcement types, the ITI was increased to a fixed 20-s duration. For the pellet group, this ITI was variably filled with the house light and reinforcer that averaged to 5 s depending on the number of pellets to be delivered, followed by a variable dark ITI that averaged 15 s. For the hopper group, as reinforcement delivery took longer, the ITI was variably filled with an average of 10 s for reinforcement delivery followed by a variable dark ITI that averaged 10 s. After 30 sessions of training, forced choice trials were added to attempt to increase contact with the contingencies of the task. Forced choice trials consisted of both the cash out and add key stimulus appearing. However, while the add key was the usual white color, the cash out key was the color associated with the minimally required number of pecks to the add key. For example, if a forced choice 3-peck trial occurred, the cash out key would appear purple while the add key appeared white. Each peck to the add key then changed the color of the add key alone, with pecks beyond the minimally required FR having no consequence.

BART. The BART task was identical to the BELT except that, in addition to the guaranteed risk of losing all accrued reward on the sixth peck, there was also an incrementing risk for each add peck beyond the first, which was always safe. The risk contingencies, shown in Table 3.1, were modeled after human experiments (e.g. Lejuez et al., 2002) such that the cumulative probability of cashing out at each number of pecks resulted in 3 pecks (half of the maximum possible) produced the optimal overall expected value. However, the local probabilities of each add key peck also had a different risk of losing on that particular peck.

Discrimination Training. Discrimination training was identical to Experiment 1 except the stimuli corresponding to the 1 and 4 reward magnitude keys were three vertical or horizontal lit lines on dark background. As every pigeon had a large side bias to the right key, the LL (4 pellets) was assigned to the left key for every pigeon while the stimulus assigned to that key was counterbalanced across birds.

Delay discounting Task. The delay discounting task was identical to Experiment 1 except the delays to the LL were shortened, systematically increasing in the order of 0, 1.5, 3, 6, and 12 s across within-session trial blocks.

Suboptimal choice Task. The suboptimal choice task was identical to Experiment 1 except that the initial link stimuli corresponding to the suboptimal and optimal alternatives were a lit leftward facing white triangle and a white lit dot on a dark background. The suboptimal alternative was assigned to the left key for half of the pigeons and to the right key for the other half with the initial link stimuli counterbalanced across subjects. The terminal links associated with the suboptimal alternative were equivalent to the previously assigned four or two pellet color in the BELT / BART tasks (i.e., red or blue) for the jackpot stimulus,

counterbalanced across subjects. The other 80% of the time the other color appeared for 10 s and signaled reward omission. The terminal links associated with the optimal alternative were followed by one of two stimuli previously associated with one or five pellets in the BELT / BART task (i.e., green or yellow) 20% of the time and the other color the remaining 80% of the time on a FT 10-s schedule. This counterbalancing was assigned so as to initially bias the pigeons towards the optimal alternative through either the stimulus that was previously associated with the greatest reward value (five pellets) or the stimulus that likely had more reinforcement history (one pellet) appearing on the optimal side.

Data Analysis. The same primary variables were used in Experiment 2 as in Experiment 1. In order to look more closely at local changes trial by trial data was accumulated. This allowed assessing an additional primary variable for the BELT and BART tasks, the coefficient of variation (CV; see Jentsch et al., 2010). This measure takes the standard deviation for the number of BELT and BART pecks across one session, respectively, and divides it by the mean for that session, generating a metric of variability in responding. This measure was theorized to assess a subject's variability in responding due to an overemphasis on local reward histories that may drive choice more analogous to real world gambling (Jentsch et al., 2010).

Descriptive statistics were again generated for each of the primary metrics and are shown in Table 3.2. There were large degrees of skewness, showing multimodal distributions that were unable to be reconciled through non-linear power transformations for the majority of the primary variables. As such, Experiment 2 used non-parametric tests to accommodate this throughout.

Results

BELT Task. Figure 3.1 illustrates the effects of signaling the number of pecks and changing the reinforcement modality had on BELT pecks per trial across acquisition (top), the frequency of each peck trial type (middle), and the number of pellets earned (bottom). As can be seen, signaling the number of pecks appeared to qualitatively increase the mean number of pecks in the pellet group relative to Experiment 1, but not the hopper group. Adding forced choice trials appeared to make little difference in either group on the average number of pecks per trial. To quantify this, a Wilcoxon signed-rank test was run for each group separately on the last 10 sessions prior to forced choice trials and the last 10 session with forced choice trials. This revealed that the average number of pecks made prior to force choice trials for the pellet ($Med = 3.78$) and hopper group ($Med = 2.31$) did not change the average number of pecks for either group (*Pellet* $Med = 3.53, Z = -0.53, p = .594$; *Hopper* $Med = 2.09, Z = -0.46, p = .646$). Spearman correlations were then run to test for consistencies in individual differences. These results showed that, for the pellet group, there was no significant correlation after adding forced choice trials, $r_s = .21, p = .205$, but there was for the hopper group, $r_s = .75, p = .013$, indicating only the hopper group showed consistent individual differences after the addition of forced choice trials.

The pellet group also appeared to both peck more and earn more reinforcers than the hopper group. Shown in the middle of Figure 3.1, during the last 10 sessions of training the hopper group had a modal peck frequency of 2 ($M = .42, SEM = .08$) while the pellet group had a modal peck frequency of 5 ($M = .32, SEM = .12$). Mann-Whitney U tests comparing each group on the average number of pecks per trial both before and after the addition of forced choice trials as well as the amount of food earned after forced choice trials were then run comparing these differences. Results showed that the pellet group made significantly

greater pecks before ($Med = 3.78$), $Z = -2.12$, $p = .034$, and after ($Med = 3.53$), $Z = -2.04$, $p = .041$, the addition of forced choice trials as well as earning more reinforcers ($Med = 125.50$), $Z = -3.67$, $p < .001$, than the hopper group ($Med = 2.31$, 2.09 and 41.25, respectively). Due to this large discrepancy in performance, the hopper group was subsequently dropped from the study and no further analysis on their data was conducted.

Spearman correlations between the primary metrics for only the pellet group were then computed. Shown in Table 3.3, it can be seen that most of the metrics were correlated with one another with the exception of BELT losses. Generally, pigeons that had greater pecks per trial also tended to cash out at higher values, were less variable in their responding, and earned more pellets. Figure 3.2 illustrates each of the significant spearman correlations along with a Pearson equivalent.

Finally, as there were significant associations with the pigeons' variability in responding (CV), trial by trial analyses were conducted to assess systematic changes in behavior. First, to look at changes across a session, a simple slope was fit to the average BELT pecks per trial within a session across the last 10 sessions of training. Shown in Figure 3.3, there appeared to be a slight increase in pecks over time; however, the slope ($s = .02$) was not significantly different from 0, $t(8) = 1.32$, $p = .188$. Sequential choice behavior was then assessed through a Wilcoxon signed-rank test on the average pecks per trial following a win versus a loss with one pigeon omitted from the analysis due to never experiencing a loss. Although there was a significant Spearman correlation, $r_s = .88$, $p = .004$, indicating the pigeons consistently made relatively high or low numbers of pecks between the two outcomes, there was no difference in the number of pecks following a win ($Med = 3.35$) or a loss ($Med = 3.84$), $Z = -1.82$, $p = .069$.

BART Task. Figure 3.4 illustrates the effects of incrementing risk on the pigeons' average pecks per trial during acquisition (top), the proportion of each peck trial type (middle), and the number of pellets earned (bottom). The pigeons' average amount of pecking was very stable across acquisition, showing little fluctuation. The modal peck frequency, however, decreased from 5 in the BELT to 1 ($M = .34$, $SEM = .13$), showing the pigeons were sensitive to the change in risk. Wilcoxon signed ranked tests further showed that BART pecks ($Med = 2.61$) and adjusted pecks ($Med = 1.99$) significantly decreased from the BELT task ($Med = 3.53, 3.30$), $Z = -2.55, p = .011$, $Z = -2.55, p = .011$, while losses significantly increased ($Bart Med = 28.80$, $BELT Med = 0.20$), $Z = -2.52, p = .012$. As shown in the bottom of Figure 3.4, the pigeons' mean number of BART pecks appeared to cluster at both 1 and 3 pecks per trial. This indicates some pigeons resorted to pecking very little in the BART task, while others may have likely been constrained by the incrementing losses limiting the birds' abilities to peck further. However, shown in the middle panel of Figure 3.4, the difference between having successfully reached a peck trial type without losing and choosing to cash out at that peck trial type also decreased with high numbers of pecks, indicating that the pigeons were sensitive to the different associations of each color and choosing to cash out proportionally more often at increasing values.

Table 3.3 further shows the Spearman correlation matrix for the primary BART variables. The BART task showed fewer within task correlations. Also illustrated in Figure 3.5 as both Spearman and Pearson correlation, it can be seen that BART pecks per trial, adjusted pecks per trial, and CV all positively correlated with BART losses regardless of the type of correlation used; however, no single variable was associated with the number of pellets earned.

To predict the number of pellets earned, two possibilities were examined. The first hypothesis essentially mirrored the curvilinear nature of the task contingencies, predicting that the number of BART and adjusted BART pecks are positively associated with pellets earned to a point where greater accumulation of losses decreases the overall pellets earned. The second hypothesis was that, rather than number of losses, variability might also negatively influence the number of pellets earned. For example, a pigeon with an average BART pecks per trial of 3 may distribute responding between a high and low amount of pecks, resulting in fewer pellets than a pigeon making a consistent number of pecks at 3 would earn.

To test the first hypothesis, multiple regression models with mean centered predictors were conducted between BART pecks per trial and BART adjusted pecks per trial in conjunction with BART losses on BART pellets earned. Shown in Tables 3.4-5, the addition of BART losses explained a significant amount of variance in both the BART pecks per trial, $F_{change}(1, 6) = 26.60, p = .002$, and the BART adjusted pecks, $F_{change}(1, 6) = 26.16, p = .002$. For the BART pecks model, both BART pecks, $t = 5.36, p = .002$, and BART losses, $t = -5.16, p = .002$, were significant predictors in the overall model, $F(2, 6) = 15.91, p = .004$. For the BART adjusted pecks model, both BART adjusted pecks, $t = 6.56, p = .001$, and BART losses, $t = -5.16, p = .002$, were significant predictors in the overall model, $F(2, 6) = 23.62, p = .001$. Finally, for each model, quadratic terms for both predictors were entered into the model. Results showed the quadratic did not explain any additional variance in the BART pecks per trial model, but the quadratic for BART losses in the BART adjusted pecks model did, $F_{change}(1, 5) = 30.68, p = .003$. In the Adjusted pecks model, Adjusted pecks, $t = 15.32, p < .001$, BART losses, $t = -13.03, p < .001$, and the quadratic BART losses term, t

= -5.54, $p = .003$, were all significant predictors in the overall model, $F(3, 5) = 103.87$, $p < .001$. As shown in Table 3.5, the negative quadratic term supported the predicted inverted U-shape association between BART adjusted pecks and BART losses, suggesting that higher BART adjusted pecks were more optimal, but to a point.

To test the second hypothesis, multiple regression interaction models were tested between BART pecks per trial and BART adjusted pecks per trial separately with BART CV on BART pellets earned. Shown in Tables 3.6-7, the addition of BART CV in step two explained a significant amount of variance in the BART adjusted pecks model, $Fchange(1, 6) = 6.04$, $p = .049$, and BART pecks model, but only the former model was significant overall. For the BART adjusted pecks model, both BART adjusted pecks, $t = 3.53$, $p = .012$, and BART CV, $t = -2.46$, $p = .049$, were significant predictors in the overall model, $F(2, 6) = 6.96$, $p = .027$. Adding the interaction term in the third step explained a significant amount of variance in both the BART pecks, $Fchange(1, 5) = 19.42$, $p = .007$, and BART adjusted pecks, $Fchange(1, 5) = 17.93$, $p = .008$, models. For the BART pecks model, only the interaction term was a significant predictor, $t = -4.41$, $p = .007$, in the overall model, $F(3, 5) = 18.21$, $p = .004$. For the BART adjusted pecks model, both BART CV, $t = -4.65$, $p = .006$, and the interaction term, $t = -4.24$, $p = .008$, were significant predictors in the overall model, $F(3, 5) = 23.72$, $p = .002$. The interactions are illustrated in Figure 3.6 with BART pellets as a function of BART pecks or adjusted pecks and CV in the left column and as predicted regression coefficients in the right column. In both cases, higher degrees of variability earned greater pellets when BART responding of either type was low; however, when BART responding was high, low variability produced greater pellets.

Finally, as the CV measure appeared to play an important role within the BART, localized analyses were again conducted similar to the BELT. First, simple slopes were fit to the average BART pecks per trial across trials to detect any changes in behavior within a session. Shown in Figure 3.7, behavior was largely stable across a session, with results showing the slope ($s = .01$) was not significantly different from zero, $t(8) = 0.59, p = .560$. A Wilcoxon signed-ranks test was also conducted on the number of BART pecks after winning ($Med = 2.76$) versus losing ($Med = 2.48$), but found no difference between the two outcomes, $Z = -1.24, p = .214$, again showing the pigeons were relatively indifferent to the local outcomes of trials.

Discrimination Training. All pigeons acquired the discrimination task of responding to the LL at least 80% of the time for three consecutive sessions ($M = 8.22, SEM = 0.89$).

Delay Discounting. As shown in Figure 3.8, most pigeons reliably chose 4 pellets over 1 at zero delay as a group. This preference then shifted to an SS preference when the LL was at 6 s ($M = 38.89, SEM = 9.97$). Although preference continued to decline at the 12 s delay, the steepness in the discounting functions appeared qualitatively shallower than in Experiment 1. Early in training, however, one bird began to develop an exclusive preference for the SS even at the 0 s delay. As such, the model was fit twice: once allowing the A parameter to vary and once with A fixed, making Equation 1 unable to estimate a k value for that bird. Table 3.8 shows the model parameters using Equation 1 to fit k ($M = 0.37, SEM = 0.12$), A ($M = 92.33, SEM = 6.28$), and AUC ($M = .16, SEM = 0.03$) parameters. Similar to Experiment 1, parameter k and AUC estimations were inversely related to one another both with, $r_s = -.98, p < .001$, and without, $r_s = 1.00, p < .001$, allowing the A parameter to vary. Model fits with Equation 1 estimating k values also described the data well with ($M r^2 = .87$,

$SEM = .01$) and without ($M = .85$, $SEM = .01$) allowing the A parameter to vary. Figure 3.9 shows two example fits with relatively higher and lower r^2 values for the sample.

Suboptimal Choice Task. Figure 3.10 shows the percent suboptimal choice across acquisition. The pigeons again began choosing the optimal alternative early, becoming indifferent between the alternatives within four sessions and showing a slight suboptimal preference by the fifth session. A criterion of 95% suboptimal choice preference over two consecutive sessions was again used and met by all birds (M sessions to criterion = 7.89, $SD = 1.30$) with individual differences in the rate of acquisition.

Between Task Associations. Further shown in Table 3.3, Spearman correlations were run between each of the task variables.

BELT and BART Tasks. Shown in Figure 3.11, there were four significant spearman correlations between the BELT and BART tasks. From the five primary variables in both tasks, the only significant between task associations was BELT losses which positively correlated with BART pecks per trial, BART losses, and BART CV. As such, pigeons that experienced more losses in the BELT task tended to also peck more, lose more, and peck more variably in the BART task.

Delay Discounting. As only two birds had A parameters not equal to 100% LL choice at 0-s delay, this parameter was not used in correlations due to spurious correlations from a lack of variability. Delay discounting k and AUC values each correlated with two variables: BELT CV and BART pecks per trial. Shown in Figure 3.12, Delay discounting k values were positively correlated with each, while AUC values were inversely correlated. This indicated that the more impulsive pigeons as assessed by the delay discounting task

tended to also have greater variability in the BELT task and peck less per trial in the BART task.

Suboptimal Choice Task. Only two variables were significantly associated with the suboptimal choice task: BELT losses and BART CV. Shown in Figure 3.13, both variables positively correlated, indicating that slower suboptimal choice acquisition was associated with greater losses in the BELT task and higher variability in BART responding.

Interactions with Delay Discounting. Similar to the previous experiments, both the BELT losses and BART CV predictors were tested for possible additive or interaction effects with delay discounting k and AUC measures. Shown in Tables 3.9-10, the addition of delay discounting k and AUC values to the BELT losses models did not explain variance on their own, but acted as suppressor variables, making the both of the overall models significant in Step II. In Step III, however, the addition of the interaction term explained a significant portion of the variance with both delay discounting k , $Fchange(1, 5) = 31.24, p = .003$, and AUC, $Fchange(1, 5) = 42.40, p = .001$, values. In the k values model, BELT losses, $t = 9.74, p < .001$, k values, $t = 3.60, p = .016$, and the interaction term, $t = 5.59, p = .003$, were all significant predictors in the overall model, $F(3, 5) = 43.73, p = .001$. In the AUC model, BART CV, $t = 11.00, p < .001$, AUC values, $t = -4.64, p = .006$, and the interaction term, $t = -6.51, p = .001$, were all significant predictors in the overall model, $F(3, 5) = 42.34, p = .001$.

The models using BART CV are shown in Tables 3.11-12. Adding both delay discounting k , $Fchange(1, 6) = 8.83, p = .025$, and AUC values, $Fchange(1, 6) = 6.73, p = .041$, explained a significant amount of variance. In the k value model, both BART CV, $t = 7.86, p < .001$, and k values, $t = 2.97, p = .025$, explained were significant predictors in the overall model, $F(2, 6) = 35.54, p < .001$. In the AUC model, both BART CV, $t = 7.65, p <$

.001, and AUC values, $t = -2.60$, $p = .041$, were significant predictors in the overall model, $F(2, 6) = 30.08$, $p = .001$. Adding the interaction term in step III also explained a significant amount of variance in both the k , $Fchange(1, 5) = 13.09$, $p = .015$, and AUC, $Fchange(1, 5) = 8.65$, $p = .032$, models. In the k value model, BART CV, $t = 10.87$, $p < .001$, k values, $t = 3.24$, $p = .023$, and the interaction term, $t = 3.62$, $p = .015$, were all significant predictors in the overall model, $F(3, 5) = 75.79$, $p < .001$. In the AUC model, BART CV, $t = 10.09$, $p < .001$, AUC values, $t = -3.13$, $p = .026$, and the interaction term, $t = -2.94$, $p = .032$, were also all significant predictors in the overall model, $F(3, 5) = 48.52$, $p < .001$.

For both the BELT losses and BART CV models, delay discounting measures showed significant moderation. Plotted both as raw data and predicted regression coefficients in Figure 3.14, it can be seen that when impulsivity levels are low, the association of increased BELT losses and BART CV is less steep than when impulsivity levels are high.

Outlier Analysis. As one bird chose the SS more than the LL even at 0 s delay after successful discrimination training, it may be argued with reason that this data point is an outlier that should not be included in the analysis. As such, outlier analyses were conducted on all of the variables with a data point greater than two standard deviations above or below the mean. Analyses were conducted through multiplying the interquartile range of the variable by the constant 2.2 (Hoaglin & Iglewicz, 1987). If any data points fell outside of that range, they were considered outliers. Indeed, bird 706 showed to be an outlier on the delay discounting A parameter as well as just outside the range for suboptimal choice acquisition.

Shown in Table 3.13 and illustrated in Figure 3.15, removing the outliers had three notable effects beyond slight changes in strengths of association noted in bold: BELT CV was no longer associated with delay discounting k or AUC values, but both BELT Losses and BART adjusted pecks per trial showed significant associations with the delay discounting metrics. Additionally, the previous interaction and additive models were no longer significant.

Discussion

The primary goal of Experiment 2 was to increase the performance of the pigeons on the BELT task when under minimal risk. This would allow us to better interpret data under conditions of greater risk without concerns about the pigeons' inability to discriminate the task contingencies. This was attempted in two ways: by signaling both the number of pecks and expected reinforcement by changing the color of the add key with each peck and by attempting to increase the discriminability of the differences in reinforcement magnitude by raising the hopper multiple times rather than presenting multiple pellets. The present experiment showed only the former to be qualitatively successful, as the hopper group in the present experiment did not appear to adequately discriminate the contingencies in the BELT task. The pellet group with the addition of signaled numbers of pecks, however, showed qualitatively increased performance of the BELT task relative to Experiment 1 with a modal peck frequency of 5 relative to 2. Additionally, this increased performance made it possible to assess an actual BART task using incrementing risk with each add key peck. In the BART task some of the pigeons continued to peck a high, near optimal number of times (about 3), whereas others pecked the add key only once or twice prior to cashing out. Greater losses in the BELT task also predicted several metrics of BART risk taking behavior including greater

pecks per trial, greater variability in responding, and greater losses. The results of the delay discounting task were also similar to that of Experiment 1 but the effect of reducing the duration of the delays showed shallower discounting effects relative to Experiment 1. Finally, the suboptimal choice task again showed rapid acquisition of a suboptimal preference resulting in a reduced level of overall food.

Similar to but more robust than Experiment 1, impulsivity as assessed by delay discounting k and AUC values appeared to be associated with performance on the BELT / BART and suboptimal choice tasks. Greater delay discounting values were associated with both greater variability in responding in the BELT task and reduced pecking in the BART task. Additionally, suboptimal choice acquisition was predicted by BELT losses as well as variability in responding in the BART task. While impulsivity levels were not directly associated with the suboptimal choice task, there was again evidence that the relationship between BELT and BART variables were moderated by impulsivity levels. However, these effects may be overly driven by one bird, as removing one subject using the outlier analyses removed these effects and the association with BELT CV, but also revealing new associations between delay discounting measures and BELT losses and BART adjusted pecks per trial.

BELT Task. Signaling the number of pecks made in the BELT task showed a qualitative improvement in the overall ability of the pigeons to maximize rewards. The modal peck frequency of the pellet group increased to 5, the optimal number of pecks; however, the use of the hopper accesses as reinforcement did not appear to be successful. It is not entirely clear why this manipulation did not work, but an over simplified description likely stems from an inability to discriminate between the different numbers of

reinforcements. This inability may have stemmed from a lack of history using multiple hoppers, reinforcement durations taking too long to assess the greater magnitudes, or perhaps perceiving each hopper reinforcement as one reinforcement. Additionally, adding forced choice trials did not increase the number of pecks made per trial in either group, suggesting they may not be necessary with this procedure.

Regardless, signaling the number of pecks and outcomes appeared to increase the discriminability of the task for the pellet group. Interestingly, however, the pigeons still showed a generally low number of losses despite the modal peck trial type being 5 and the average pecks per trial being nearly 1 peck greater on average relative to Experiment 2. Indeed, some pigeons in the present experiment pecked many times on the add key but very rarely lost, while others pecked a similar number of times but lost more often. As such, BELT losses continued to be an important predictor in the present experiment despite these low frequencies, predicting both performance on BART and suboptimal choice measures. Despite the frequencies of BELT losses being important predictors, the actual loss itself again seemed to have little effect on behavior as the number of pecks following a loss was not significantly different from those following a win. Additionally, there were no systematic changes in behavior as a function of trial within a session. However, variability in responding was also an important predictor, negatively correlated with pecks per trial, adjusted pecks, and the amount of pellets earned, suggesting that the way in which pigeons responded to local trial outcomes was important, but no evidence of systematic variation was found.

BART task. With the improved performance on the BELT task, it was possible to assess the effects of increasing the amount of risk per add key peck on number of pecks per

trial. Incrementing the risk showed a significant decrease in both the number of pecks, adjusted pecks, and an increase in losses on the BART task, indicating the pigeons were sensitive to the change. Despite this, many of the pigeons in the present task still pecked near the optimal number of times (3 per trial). The average number of pecks per trial following a loss was also not significantly different following a win, nor was there any systematic change in behavior across trials within a session, again suggesting relative risk tolerance at asymptotic levels of performance. This suggests that pigeons, unlike humans (Lejuez et al., 2002) and rats (Jentsch et al., 2010), may be less risk averse, at least with this task. It should be noted, however, that the present experiment may have initially biased the pigeons by giving them sufficient experience under low risk conditions in the BELT, which was an opportunity often not available with other procedures.

Additionally, it can be seen from the bottom of Figure 12 that many pigeons did not earn an optimal number of pellets. Indeed, some pigeons that pecked close to the optimal number of times actually obtained the same or fewer reinforcements than pigeons pecking only once or twice per trial. This may have resulted from biasing the pigeons in the BELT task to peck more often on average, leading to sustained large number of pecks but not optimal performance. The results similarly showed that no single predictor in the BART predicted number pellets earned, but that more pecks and adjusted pecks per trial were beneficial to a point where the greater accumulation of losses made it no longer optimal. Perhaps more interesting, though, was the significant interaction between number of pecks and adjusted pecks with CV on pellets earned. This revealed that greater variability was beneficial when the average number of pecks was low, but detrimental when it was high, illustrating a situation analogous to the concept of *exploration and exploitation* (Humphreys

et al., 2015; Rolison et al., 2012). That is, the pigeons that tended to earn more food explored different number of pecks over trials when responding was low, but exploited a particular strategy when the average amount of responding was high, suggesting that learning plays an important role in this task.

Delay discounting task. Most birds again showed the expected pattern of devaluing the LL reward as the delay to that reinforcer increased. Initially there was an LL preference that decreased to an SS preference at a 6 s delay to the LL. Additionally, discounting k and AUC values showed the expected inverse relationship. Despite all of the birds successfully discriminating 1 from 4 pellets in the discrimination training phase, one bird showed an SS preference even when the delay to 4 pellets was 0 s. This bird continued, however, to show a decreasing preference for the LL as its delay increased similar to the others. As such, one possibility may be that this bird generalized delays across the blocks of training or that the LL took on an aversive value even with no delays. This could potentially justify not removing the bird's data from the analysis, although the interpretation may need to be altered from that of discounting the delayed reward (i.e., impulsivity) to a simpler greater sensitivity to delayed reinforcement.

Suboptimal choice task. Preferences in the suboptimal choice task again showed an initial preference for the optimal alternative similar to previous research (Laude, Beckmann, et al., 2014) but acquired a suboptimal preference quickly. Only one bird took notably longer to acquire a suboptimal preference and was removed according to the outlier analysis.

Between task associations. BELT losses were significantly associated with BART pecks per trial, variability in responding, and losses, implicating that performance on the BELT task with low levels of risk may be able to predict performance with high risk in the

BART task. However, neither number of pecks or adjusted pecks per trial measures correlated between the BELT and BART tasks. One interpretation of these data might be that the ability to discriminate outcomes in the BELT task (pecking close to 5 times per trial) and loss tolerance may be separate dimensions of this task. That is, it is possible to perform optimally in the BELT task without experiencing many losses, but to perform optimally in the current BART task (pecking 3 times per trial) requires both high discriminability of outcomes as well as losing approximately 40% of the time.

The results of Experiment 2 also showed that greater impulsivity as assessed by delay discounting k values was positively associated (and AUC values negatively associated) with variability in BELT responding. While this relationship was no longer significant when outliers were removed, an inverse association between discounting was then found with fewer BELT losses (and positively associated with AUC values). The former association seems to suggest that greater impulsivity levels were associated with greater variability in responding, potentially indicating more impulsive pigeons were less likely to exploit a particular choice strategy. Additionally, the greatest potential for variability in responding occurs when responses average to moderate amounts of the potential number of pecks. This may indicate why BELT losses were also inversely associated with the removal of outliers (but not BELT pecks), as high degrees of variability may have coincided with only moderate levels of pecks per trial, resulting in fewer losses, but were not high enough to show a significant correlation with BELT pecks.

This interpretation is also substantiated by the negative correlation between BART pecks per trial, losses, and k values (and positive correlation with AUC values), which suggests that greater impulsivity levels were associated with fewer numbers of overall pecks

and, correspondingly, losses. These associations were also maintained when outliers were removed, with BART adjusted pecks now also showing a similar association. Together, these correlations suggest that under conditions of high risk, more impulsive birds pecked only a few times prior to cashing out. It remains to be explained, however, why this might be. Increased discounting suggests that it may be due to the greater delay of gratification associated with larger magnitude outcomes (Odum, 2011); however, it may also work in conjunction with the cash out key serving as a lower order conditioned reinforcer relative to the add key, potentially driving choice to peck only a few times in order to obtain reward as soon as possible. Additionally, delay discounting variables again showed no direct relationship with suboptimal choice acquisition, discordant with the results of Laude, Beckmann, et al. (2014). This discrepancy is likely due to the same reasons noted in Experiment 1: namely the differences in visual vs. spatial discriminations and comparing asymptotic preferences vs. speed of acquisition.

Experiment 2 also showed similarities to Experiment 1 in that the BELT task was significantly associated with the acquisition of suboptimal choice. Indeed, BELT losses showed a positive correlation with suboptimal choice indicating greater numbers of losses were associated with slower acquisition. This relationship is opposite to that found in Experiment 1, however, which showed greater BELT losses were associated with faster acquisition. The added predictor of BART variability in responding also showed the same positive correlation with suboptimal choice acquisition, opposite to the predicted direction from Experiment 1. This measure is difficult to interpret, however, as the previously noted interaction when predicting BART pellets showed that BART variability can be both beneficial and detrimental at low vs. high amounts of responding, respectively. One

parsimonious account of these data might be that pigeons that were less able to discriminate the contingencies of the BELT and BART tasks were also slower to acquire the suboptimal choice task. That is, as Experiment 2 signaled the number of pecks, this allowed some pigeons to perform near optimally in the BELT task while experiencing few losses.

However, pigeons that were less able to discriminate when to cease responding in the BELT task or exploit a consistent strategy on the BART task (high variability) may have been doing so somewhat indiscriminately. This then may show similar indiscriminate responding and slowed acquisition of a suboptimal choice preference if these pigeons were less sensitive to the contingencies in each task.

Additionally, if outliers were not removed from the dataset, the significant interactions showed that delay discounting variables moderated these associations between BELT losses, BART CV, and suboptimal choice acquisition. When discounting was high in conjunction with high values on either BELT losses or BART CV acquisition was slower while under the same conditions as when discounting levels were relatively lower. This finding may also be congruent with the previous interpretations of the discounting and BELT / BART variables as Jentsch et al. (2010) implicated variability in responding as due to a lack of self-control over behavior. Through reducing activity in the medial prefrontal cortex through a GABA agonist, Jentsch et al. (2010) showed that variability increased independently of other similar mechanisms such as incentive salience towards food rewards. Likewise, human fMRI data implicated the analogous dorsolateral prefrontal cortex region in the expression self-controlled decisions (Hare, Camerer, & Rangel, 2009). Thus, high impulsivity in conjunction with high BART variability predicting slower suboptimal choice

acquisition, both previously implicated in lack of behavioral control, may suggest indiscriminate responding in these tasks.

The results of Experiment 2 both expanded on Experiment 1 and confirmed some of the a priori hypotheses. These differences in associations between the experiments seem likely due to the signaling of the outcomes which improved performance and may have allowed for greater distinguishing between high and low performing pigeons. The results showed significant associations between variables in the BELT, BART, delay discounting, and suboptimal choice tasks. Some of these predictions, such as those between BELT losses and BART CV with slower suboptimal choice acquisition, were not in the expected direction. These associations, however, appear to be more complex than simple correlations can explain, necessitating future research to examine these questions with sufficient power to assess them. For example, many other correlations shown in Table 3.3 were relatively high, but not high enough given the small sample in the present experiment. Additionally, the violations of normality within the dataset further complicate the picture. Finally, future studies may wish to further increase the potential for responding in BELT and BART tasks. As signaling the number of pecks appeared to substantially increase the number of pecks made, it seems possible to extend this range beyond six using different stimuli with each peck in order to help the pigeon discriminate how many responses have been made. Indeed, these different signals may also be analogous to the visual stimuli of the both the balloon and local reward tracker seen in human experiments that may help them discriminate their progress (Lejuez et al., 2002) and thus may make the results more generalizable.

Table 3.1. Design parameters for the BART task. *Note:* the bolded column indicates the optimal point of responding.

Add Key Responses	1	2	3	4	5	6
Cumulative p(Win)	100%	80%	60%	40%	20%	0%
Local p(Win)	100%	80%	75%	67%	50%	0%
Expected Value	1	1.6	1.8	1.6	1	0

Table 3.2. Descriptive statistics for the primary variables in Experiment 2 both before and after a square root transform was applied. Normality was assessed according to a Shapiro-Wilks test.

	Raw Scores Mean (95% CI)	Normality <i>p</i> -value (n)	Square Root Mean (95% CI)	Normality <i>p</i> -value (n)
BELT Pecks per Trial	3.52 (2.52-4.52)	< .001 (90)	—	—
BELT Adjusted Pecks per Trial	3.43 (2.45-4.40)	< .001 (90)	—	—
BELT Pellets	124.24 (106.99-141.49)	.001 (90)	—	—
BELT Losses	1.07 (-0.09-2.23)	< .001 (90)	—	—
BELT CV	0.29 (0.13-0.46)	< .001 (90)	—	—
BART Pecks per Trial	2.14 (1.39-2.89)	< .001 (90)	—	—
BART Adjusted Pecks per Trial	1.98 (1.27-2.69)	< .001 (90)	—	—
BART Pellets	68.00 (59.12-76.88)	< .001 (90)	—	—
BART Losses	19.04 (6.10-31.97)	< .001 (90)	—	—
BARTCV	0.28 (0.07-0.48)	< .001 (90)	—	—
Delay Discounting <i>k</i> values	0.54 (0.30-0.77)	.019 (9)	0.71 (0.55-0.86)	.389 (9)
Delay Disocunting A values	92.33 (76.98-107.68)	< .001 (9)	—	—
Delay Discounting AUC	0.50 (0.33-0.68)	.361 (9)	—	—
Sub-optimal Choice Criterion	7.89 (4.71-11.07)	.003 (9)	—	—

Table 3.3. Spearman correlation matrix for the primary variables between all tasks in Experiment 2.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
BELT Pecks per Trial ¹	—													
BELT Adjusted Pecks per Trial ²	.93***	—												
BELT Pellets ³	.88**	.97***	—											
BELT Losses ⁴	.49	.26	.14	—										
BELT CV ⁵	-.73*	-.77*	-.80**	-.30	—									
BART Pecks per Trial ⁶	.45	.28	.20	.73*	-.45	—								
BART Adjusted Pecks per Trial ⁷	.33	.25	.17	.64	-.42	.95***	—							
BART Pellets ⁸	-0.32	-.17	-.17	-.08	-.07	.42	.63	—						
BART Losses ⁹	0.53	.35	.25	.85***	-.53	.95***	.88**	.25	—					
BART CV ¹⁰	.18	-.08	-.20	.91**	.00	.62	.57	-.03	.72*	—				

Table 3.3 (continued)

Delay Discounting k values ¹¹	-.47	-.40	-.38	-.39	.72*	-.72*	-.60	-.25	.72*	-.12	—			
Delay Discounting A values ¹²	.27	.39	.50	.02	-.73*	.27	.27	.32	.27	-.27	-.73*	—		
Delay Discounting AUC ¹³	.52	.43	.40	.50	-.70*	.77*	.65	.23	.77*	.22	-.98***	.71*	—	
Sub-optimal Choice Criterion ¹⁴	.15	-.09	-.18	.88**	.06	.38	.32	-.21	.55	.91**	-.03	-.19	.15	—

Table 3.4. Polynomial model between BART pecks per trial and losses on BART pellets earned.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.02	–
BARTppt	4.39	-5.41 – 14.19	.14	–	–
Step II:	–	–	–	.79**	.77**
BARTppt	104.06**	56.54 – 151.59	.76	–	–
BARTLoss	-5.82**	-8.58 – -3.06	.70	–	–
Step III:	–	–	–	.81*	.02
BARTppt	84.51*	2.80 – 166.22	.20	–	–
BARTLoss	-4.78*	-9.49 – -0.06	.19	–	–
BARTppt ²	-0.07	-0.23 – 0.10	.03	–	–
BARTLosses ²	9.76	-34.16 – 53.69	.01	–	–

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 3.5. Polynomial model between BART adjusted pecks per trial and losses on BART pellets earned.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.31	–
AdjBARTppt	7.87	-0.82 – 16.56	.40	–	–
Step II:	–	–	–	.85***	.54**
AdjBARTppt	27.39***	17.15 – 37.62	.80	–	–
BARTLoss	-1.17**	-1.74 – 0.61	.49	–	–
Step III:	–	–	–	.98***	.14**
AdjBARTppt	26.41***	21.98 – 30.85	.74	–	–
AdjBARTLoss	-1.23***	-1.48 – -0.99	.56	–	–
BARTLosses ²	-0.04**	-0.06 – -0.02	.10	–	–

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 3.6. Polynomial model between BART pecks per trial and CV on BART pellets earned.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.02	–
BARTppt	4.39	-5.41 – 14.19	.14	–	–
Step II:	–	–	–	.45	.43*
BARTppt	11.15*	1.24 – 21.07	.52	–	–
BARTCV	-38.60*	-75.29 – -1.91	.45	–	–
Step III:	–	–	–	.87**	.42**
BARTppt	1.63	-5.96 – 9.21	.01	–	–
BARTCV	-7.44	-33.81 – 18.94	.01	–	–
BARTppt*BARTCV	62.18**	-98.45 – -25.91	.33	–	–

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 3.7. Polynomial model between BART adjusted pecks per trial and CV on BART pellets earned.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.31	–
AdjBARTppt	7.87	-0.82 – 16.56	.40	–	–
Step II:	–	–	–	.60*	.29*
AdjBARTppt	10.69*	3.28 – 18.10	.63	–	–
BARTCV	-25.98	-51.85 – -0.11	.30	–	–
Step III:	–	–	–	.90**	.30**
AdjBARTppt	1.04	-6.04 – 8.12	.00	–	–
BARTCV	25.15**	-39.06 – -11.24	.28	–	–
AdjBARTppt*BARTCV	79.95**	-128.48 – 31.42	.24	–	–

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 3.8. Parameter estimates for Delay Discounting k values with the A parameter fixed and adjusted and area under the curve values for the delay discounting task.

Bird	DDk adjusted	SqrtDDk	A	r²	DDk fixed	r²	DDauc
1	0.057	0.239	100.00	0.887	0.057	0.887	0.124
706	1.070	1.034	39.63	0.941			0.078
712	0.081	0.284	100.00	0.858	0.081	0.858	0.120
719	0.255	0.505	100.00	0.826	0.255	0.826	0.101
728	0.188	0.433	100.00	0.862	0.188	0.862	0.156
1886	0.045	0.213	100.00	0.865	0.045	0.865	0.161
19243	0.201	0.448	100.00	0.868	0.201	0.868	0.358
19276	0.480	0.693	100.00	0.808	0.480	0.808	0.082
19849	0.953	0.976	91.34	0.953	0.975	0.839	0.221

Table 3.9. Regression interaction model of BELT Losses and delay discounting k values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.35	–
BELTLoss	1.80	-0.06 – 3.66	.43	–	–
Step II:	–	–	–	.60*	.25
BELTLoss	2.15*	0.60 – 3.71	.58	–	–
DD k	10.82	-0.65 – 22.29	.27	–	–
Step III:	–	–	–	.93***	.33**
BELTLoss	2.69***	1.98 – 3.40	.79	–	–
DD k	7.25*	2.07 – 12.42	.11	–	–
BELTLoss*DD k	7.00**	3.78 – 10.21	.26	–	–

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 3.10. Regression interaction model of BELT Losses and delay discounting AUC values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.35	–
BELTLoss	1.80	-0.06 – 3.66	.43	–	–
Step II:	–	–	–	.52*	.17
BELTLoss	2.35*	0.56 – 4.15	.61	–	–
DDauc	-9.03	-20.78 – 2.72	.21	–	–
Step III:	–	–	–	.94***	.42***
BELTLoss	3.23***	2.48 – 3.99	.92	–	–
DDauc	-7.97**	-12.38 – -3.55	.16	–	–
BELTLoss*DDauc	7.02***	-9.79 – -4.25	.32	–	–

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 3.11. Regression interaction model of BART CV and delay discounting k values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.78***	–
BARTCV	14.06***	7.93 – 20.20	.81	–	–
Step II:	–	–	–	.90***	.12*
BARTCV	14.01***	9.65 – 18.37	.80	–	–
DD k	6.87*	1.21 – 12.52	.11	–	–
Step III:	–	–	–	.97*	.07*
BARTCV	12.30***	9.39 – 15.20	.51	–	–
DD k	4.72*	0.98 – 8.47	.05	–	–
BARTCV*DD k	17.38*	5.03 – 29.74	.06	–	–

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 3.12. Regression interaction model of BART CV and delay discounting AUC values predicting suboptimal choice acquisition.

Variables	B	95% CI	sr ²	Adj R ²	ΔAdj R ²
Step I:	–	–	–	.78***	–
BARTCV	14.06***	7.93 – 20.20	.81	–	–
Step II:	–	–	–	.88***	.10*
BARTCV	14.93***	10.15 – 19.70	.88	–	–
DDauc	-5.83*	-11.32 – -0.33	.10	–	–
Step III:	–	–	–	.95***	.07*
BARTCV	13.71***	10.21 – 17.20	.68	–	–
DDauc	-4.79*	-8.72 – -0.85	.07	–	–
BARTCV*DDauc	-16.37*	-30.67 – -2.07	.06	–	–

* $p \leq .05$, ** $p \leq .01$, *** $p \leq .001$

Table 3.13. Spearman correlation matrix for the primary variables between all tasks in Experiment 2 after removing outliers.

	1	2	3	4	5	6	7	8	9	10	11	12	13
BELT Pecks per Trial ¹	—												
BELT Adjusted Pecks per Trial ²	—	—											
BELT Pellets ³	—	—	—										
BELT Losses ⁴	—	—	—	—									
BELT CV ⁵	—	—	—	—	—								
BART Pecks per Trial ⁶	—	—	—	—	—	—							
BART Adjusted Pecks per Trial ⁷	—	—	—	—	—	—	—						
BART Pellets ⁸	—	—	—	—	—	—	—	—					
BART Losses ⁹	—	—	—	—	—	—	—	—	—				
BART CV ¹⁰	—	—	—	—	—	—	—	—	—	—			

Table 3.13 (continued)

Delay Discounting k values ¹¹	-.55	-.36	-.26	-.79*	.60	-.88**	-.71*	-.17	-.88**	-.60	—		
Delay Discounting AUC ¹²	.55	.36	.26	.79*	-.60	.88**	.71*	.17	.88**	.60	1***	—	
Sub-optimal Choice Criterion ¹³	.22	.01	-.07	.85**	.06	.44	.36	-.06	.68	.87**	-.48	.48	—

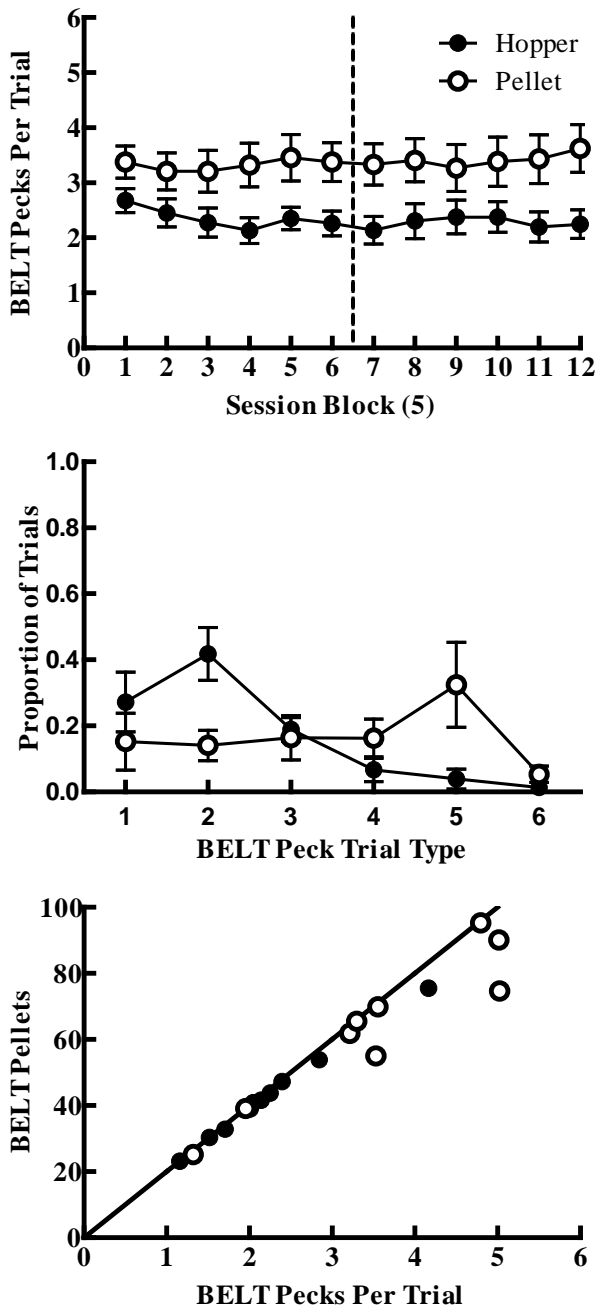


Figure 3.1. **Top.** Mean (\pm SEM) BELT pecks per trial across acquisition. The dotted line indicates the point at which forced choice trials were introduced. **Middle.** Mean (\pm SEM) peck trial type frequency averaged over the last 10 sessions. **Bottom.** Total pellets earned as a function of the pigeons' average BELT pecks per trial over the last 10 sessions where the black line indicates total possible reinforcements.

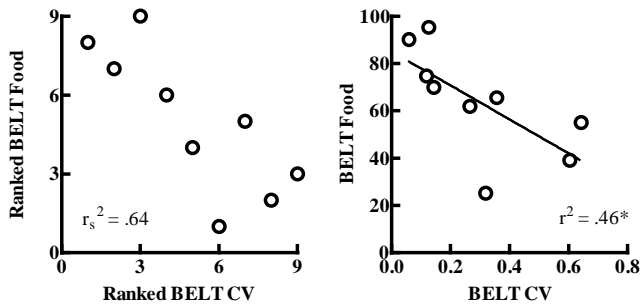
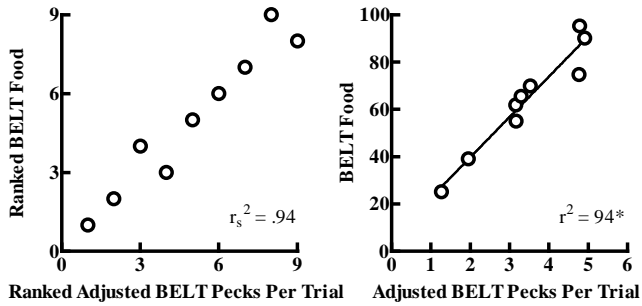
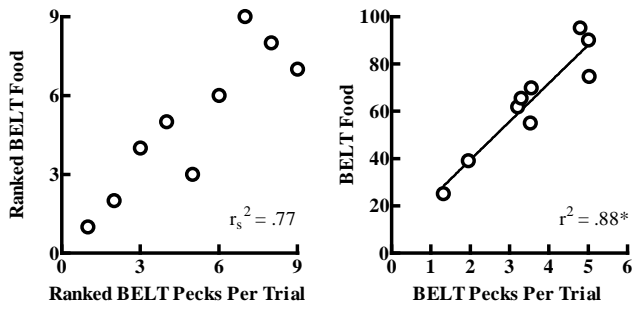
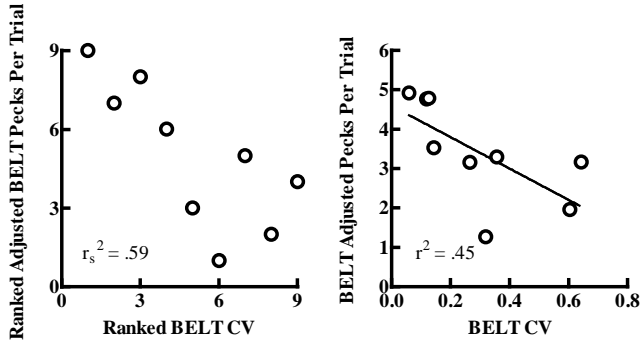
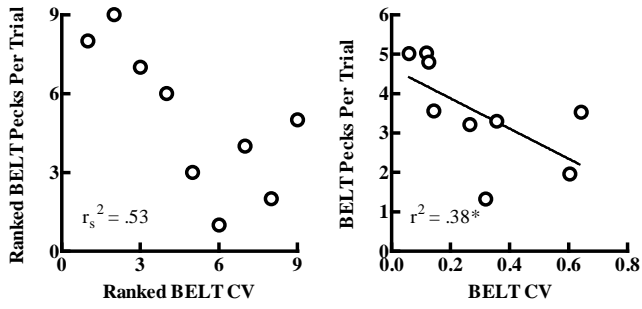


Figure 3.2. Left Column. Significant spearman correlations between primary BELT variables. **Right Column.** Pearson correlation between primary BELT metrics with best fitting regression line. *Note:* * indicates $p \leq .05$.

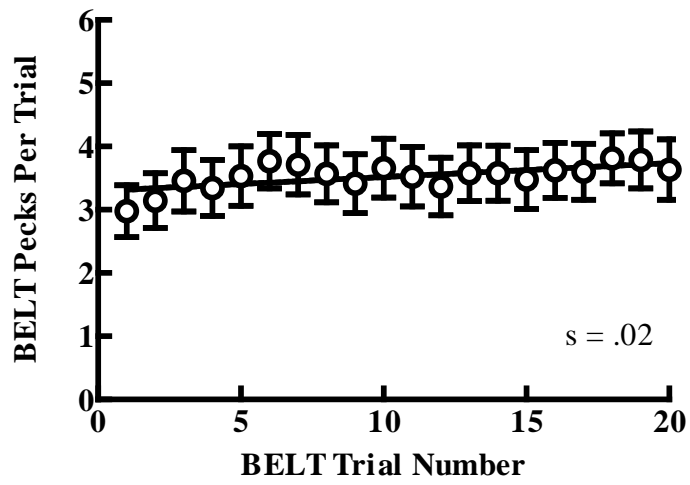


Figure 3.3. Mean (\pm SEM) BELT pecks per trial across free choice trials.

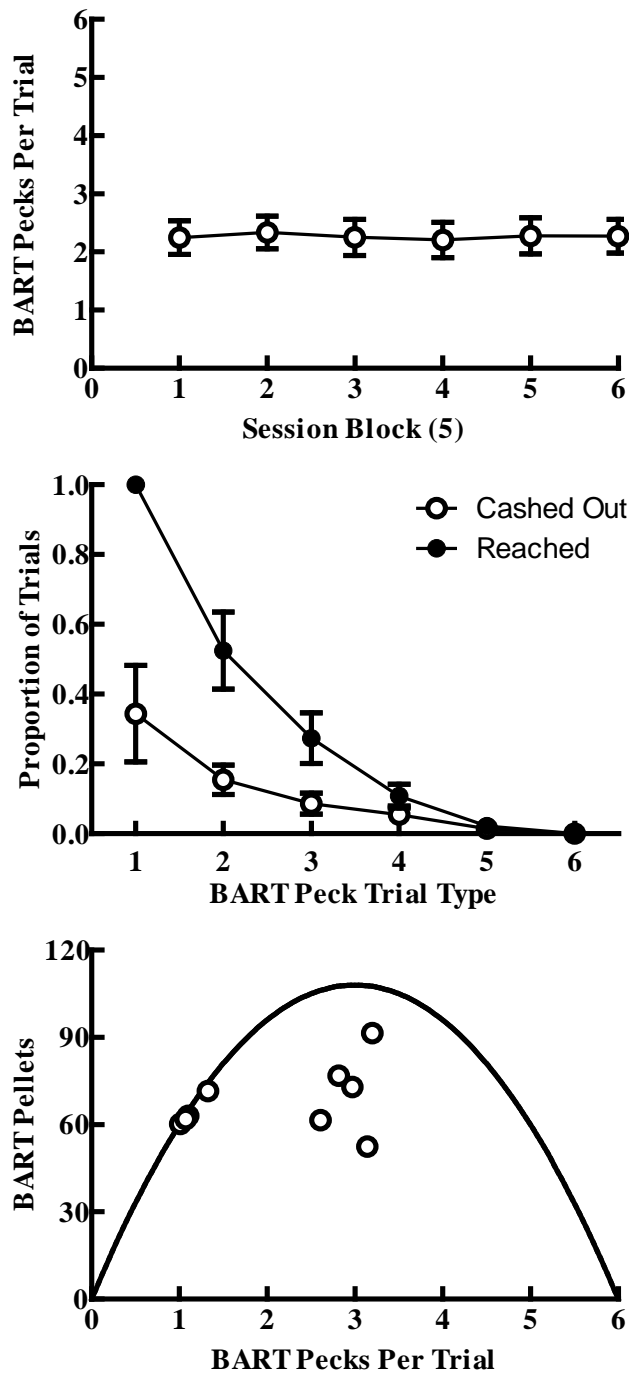


Figure 3.4. **Top.** Mean (\pm SEM) BART pecks per trial across acquisition. **Middle.** Mean (\pm SEM) peck trial type frequency averaged over the last 10 sessions. **Bottom.** Total pellets earned as a function of the pigeons' average BART pecks per trial over the last 10 sessions where the black line indicates total possible reinforcements.

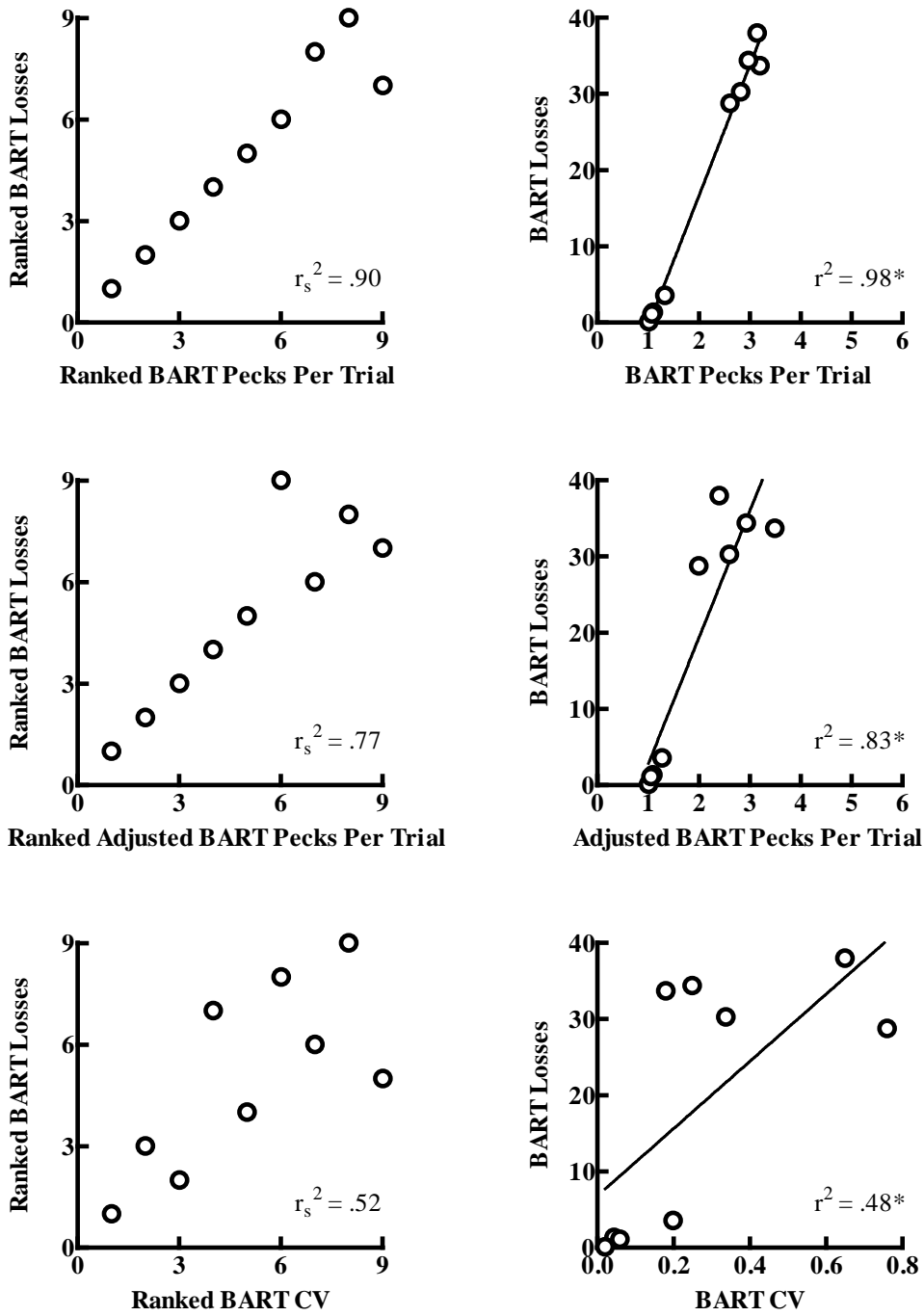


Figure 3.5. **Left Column.** Spearman correlations between primary BART variables. **Right Column.** Pearson correlation between primary BART variables with best fitting regression line. Note: * indicates $p \leq .05$.

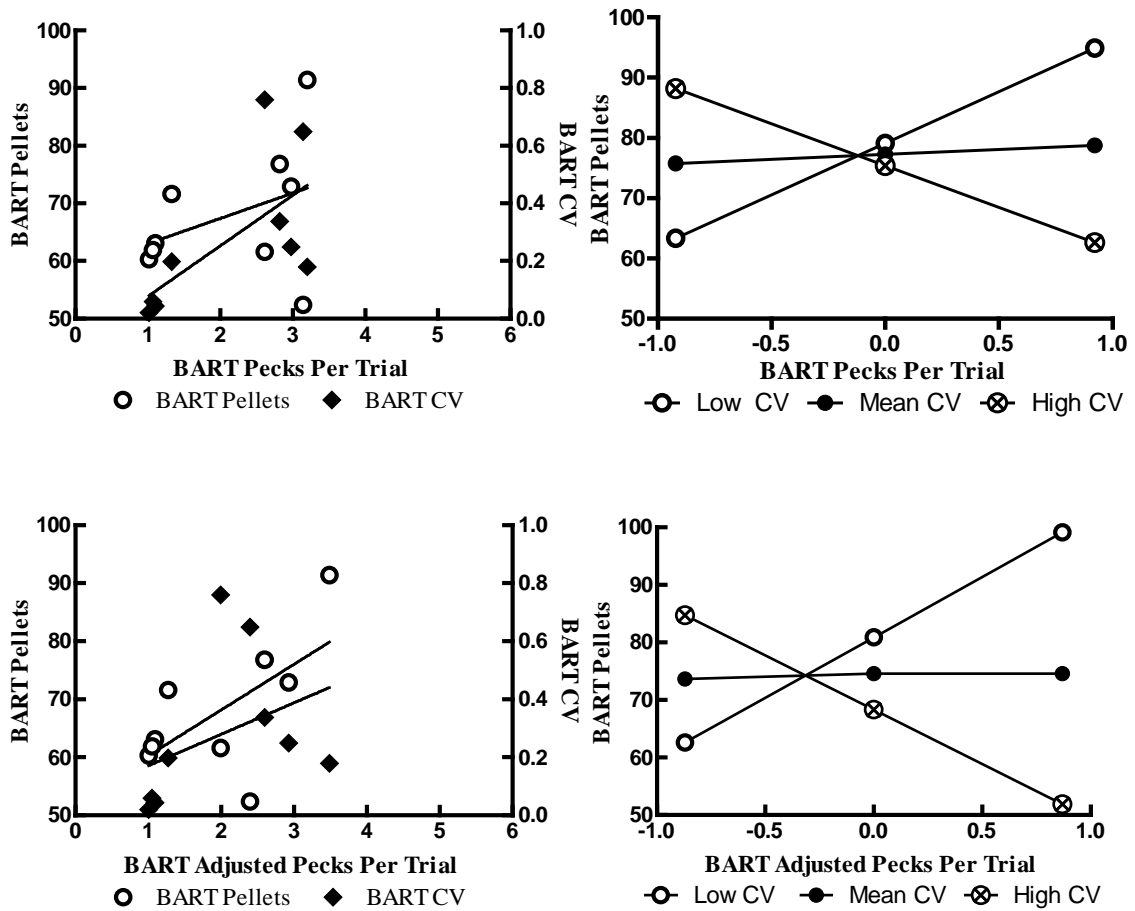


Figure 3.6 . Left Column. Interaction effects of BART pellets and CV as a function of BART pecks per trial (top) and adjusted pecks per trial (bottom). **Right Column.** Predicted values of BART pellets as a function of mean centered BART pecks per trial at low, medium, and high CV values as a function of BART pecks per trial and (top) and as a function of adjusted pecks per trial (bottom).

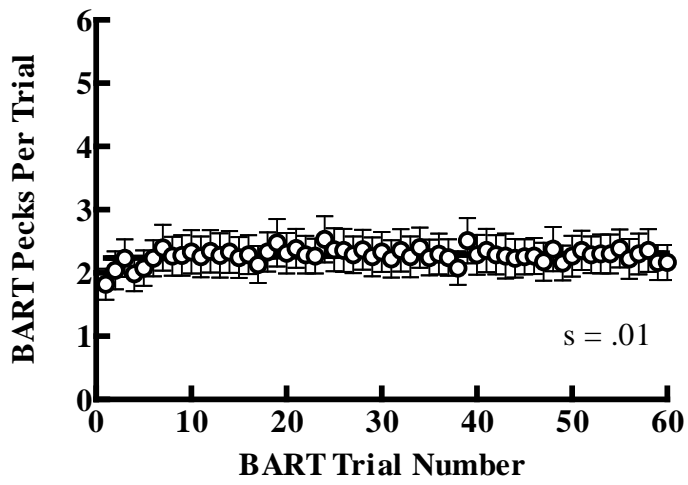


Figure 3.7. Mean (\pm SEM) BART pecks per trial averaged over the last 10 sessions of training.

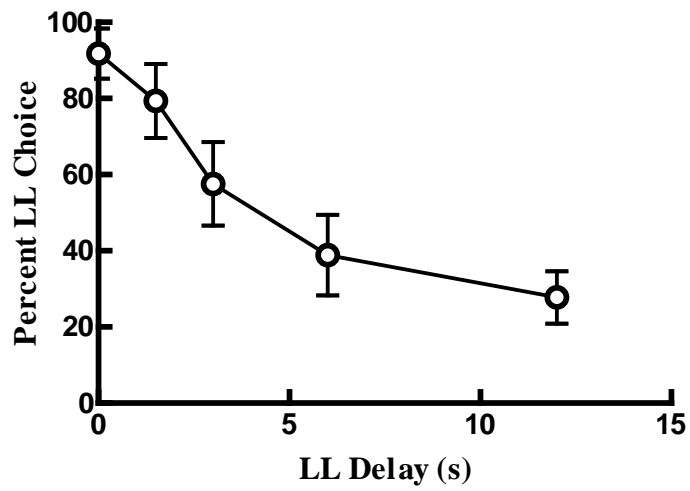


Figure 3.8. Mean (\pm SEM) percent LL choice over the last 10 sessions of training in the delay discounting task.

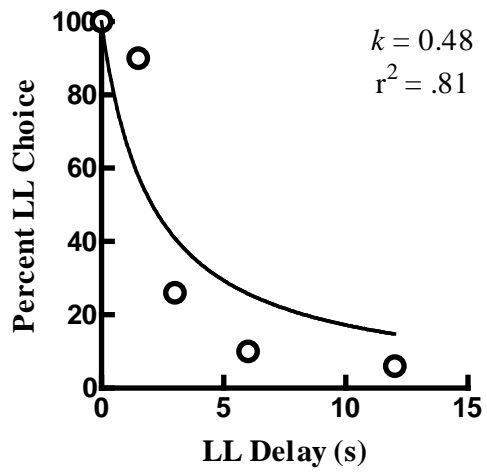
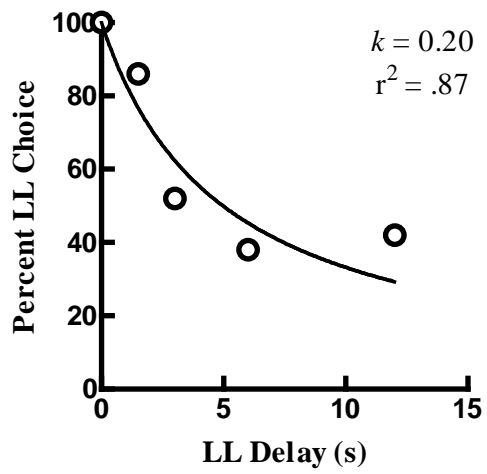


Figure 3.9. Example adjusted k parameter fits using equation 1 for birds 19243 (top) and 19276 (bottom).

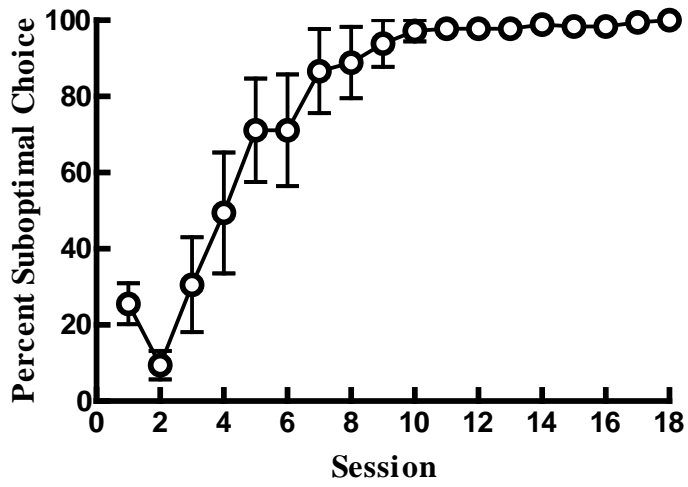


Figure 3.10. Mean (\pm SEM) percent choice of the suboptimal alternative across the 18 sessions of training.

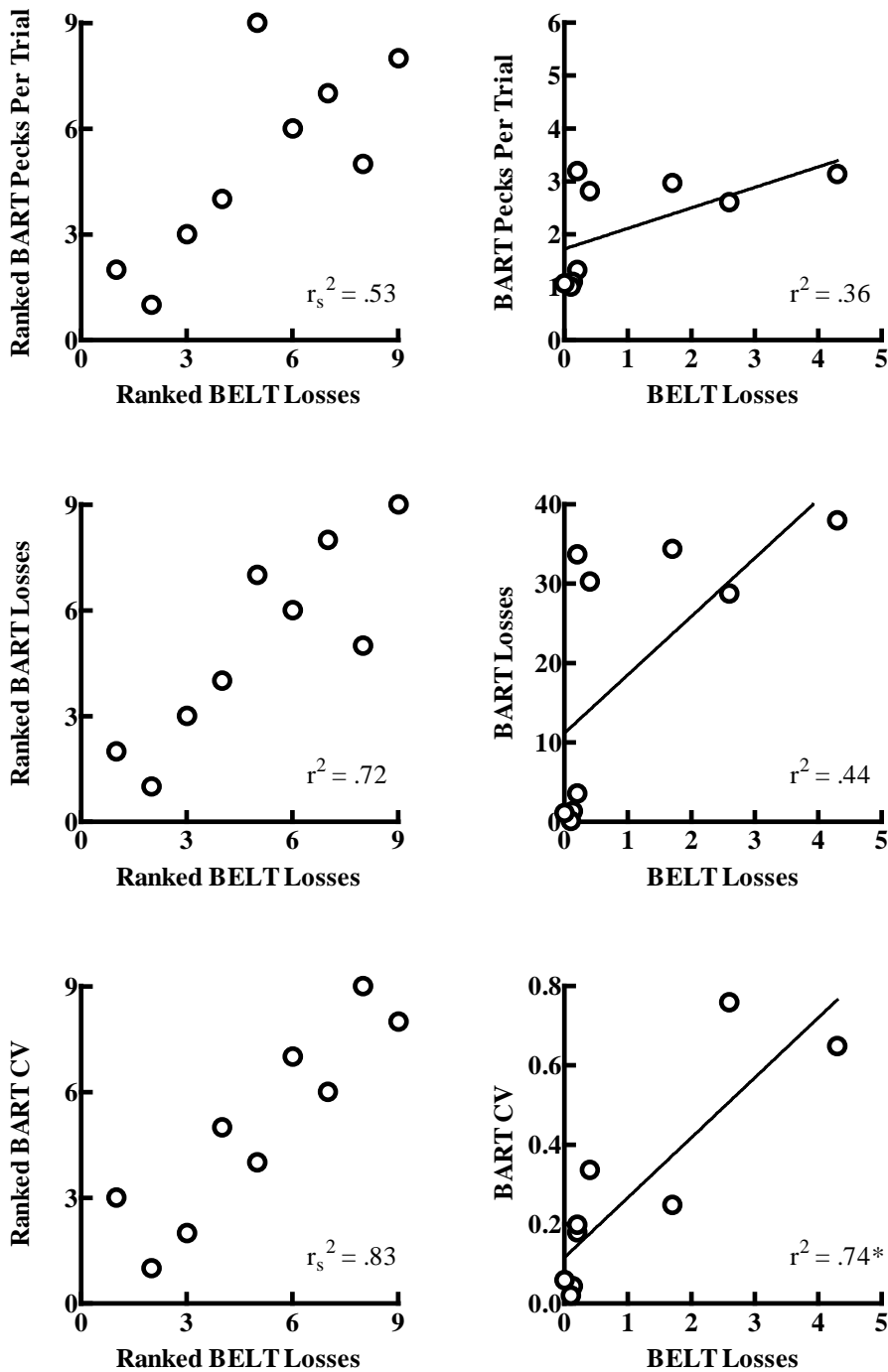


Figure 3.11. **Left Column.** Significant Spearman ranked correlations between the BELT and BART task in Experiment 2. **Right Column.** Pearson correlations with regression line of best fit between the BELT and BART task in Experiment 2. Note: * indicates $p \leq .05$.

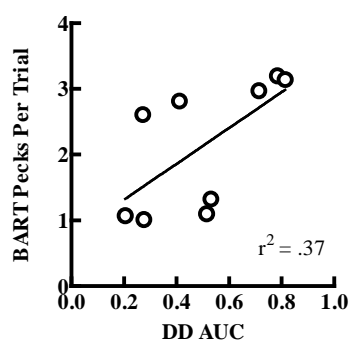
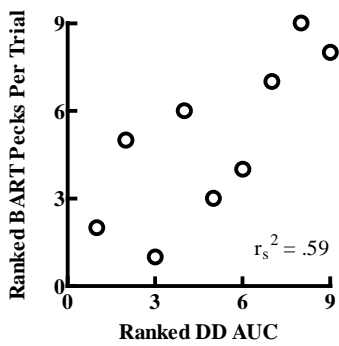
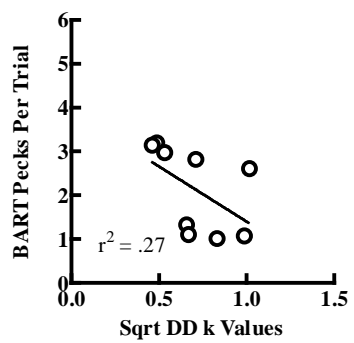
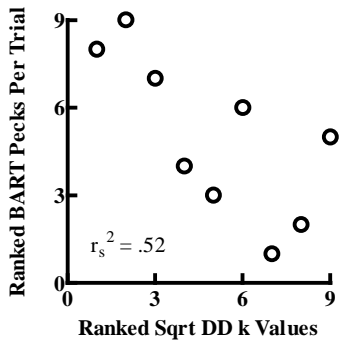
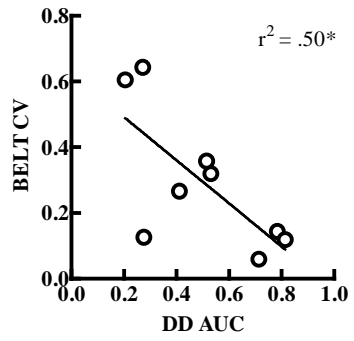
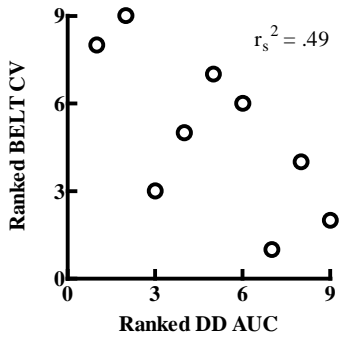
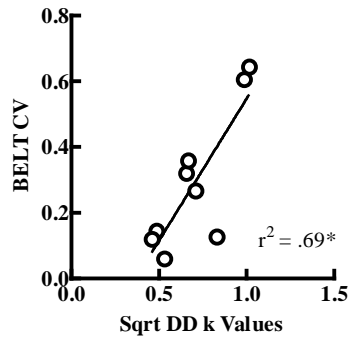
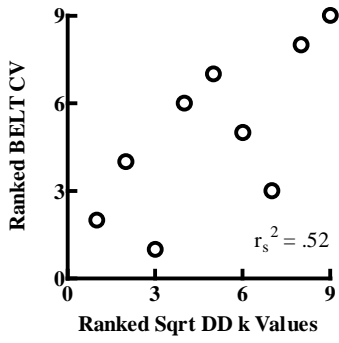


Figure 3.12. Left Column. Significant Spearman ranked correlations between the delay discounting k and AUC values and BART and BELT performance. **Right Column.** Pearson correlations with linear regression line of best fit between the delay discounting k and AUC values and BART and BELT performance. *Note:* * indicates $p \leq .05$.

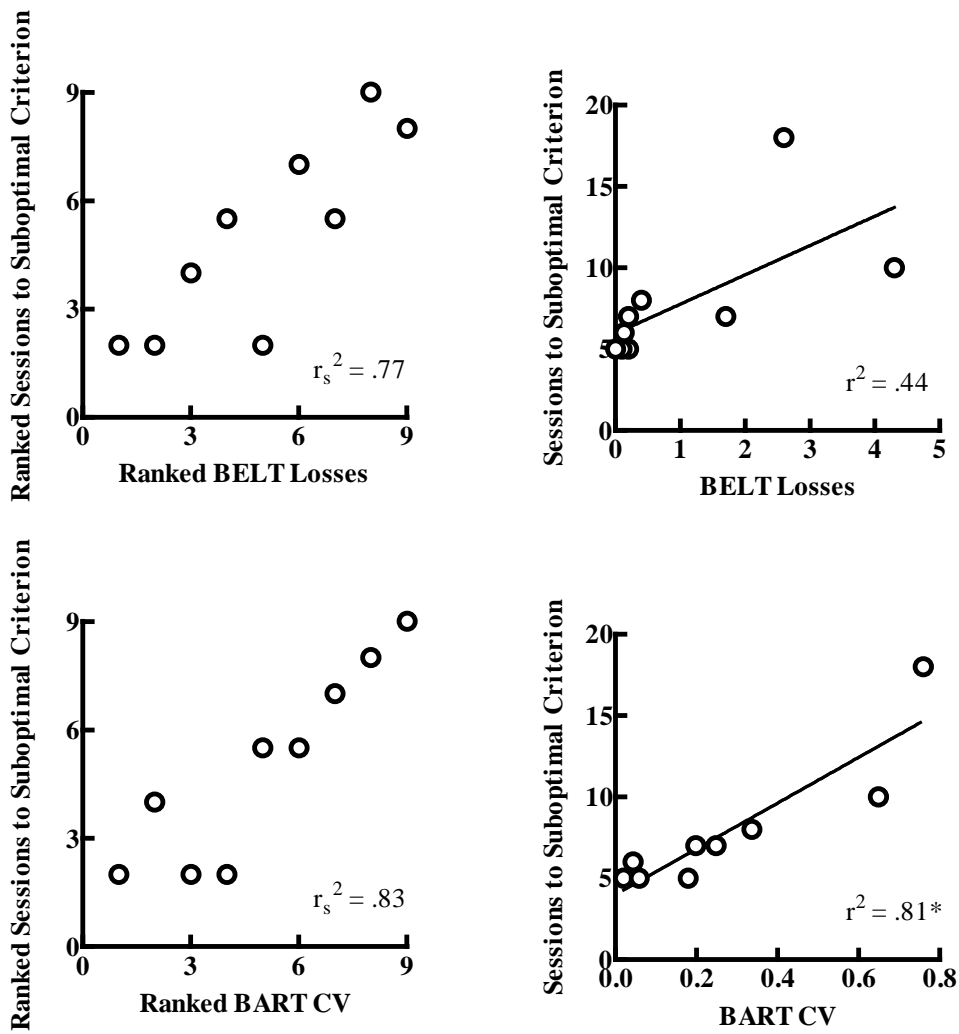


Figure 3.13. Left Column. Significant Spearman ranked correlations between BELT and BART performance and Suboptimal Choice Acquisition. Right Column. Pearson correlations with linear regression line of best fit.

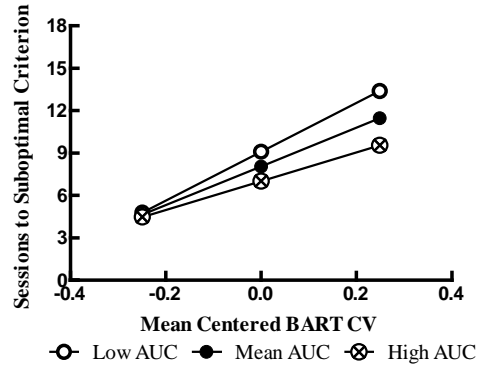
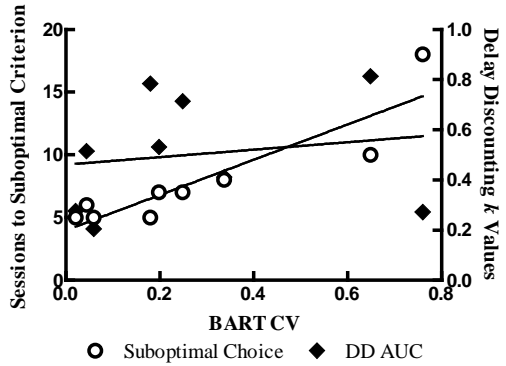
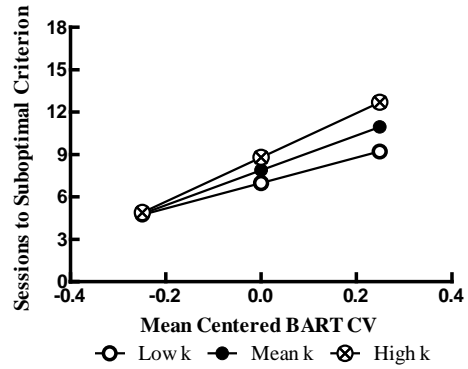
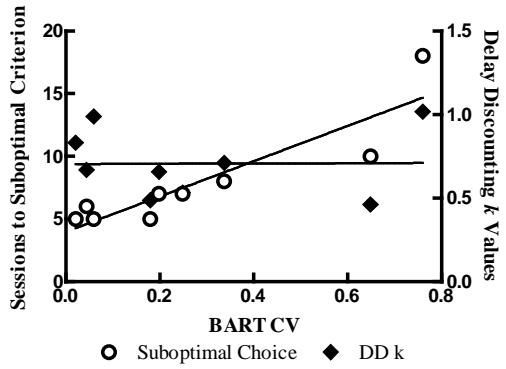
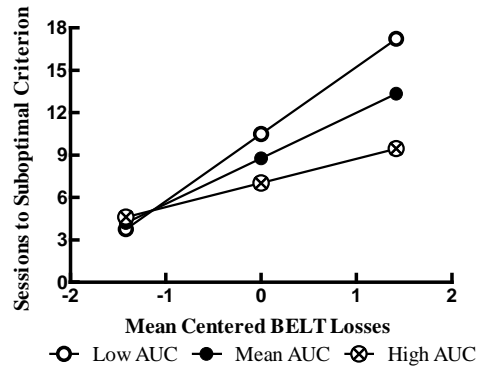
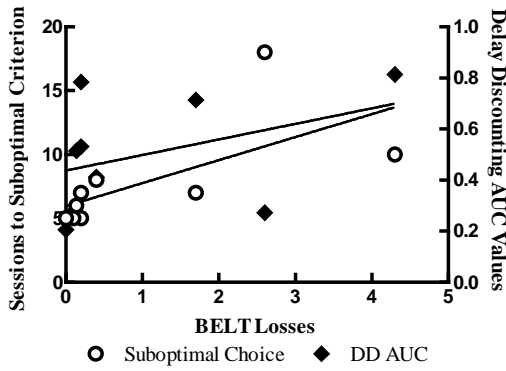
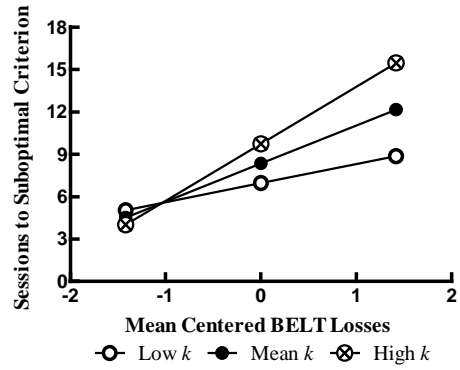
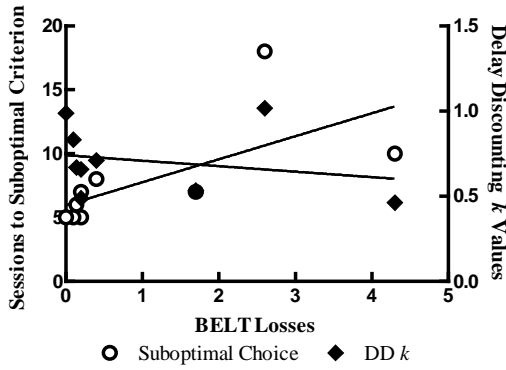


Figure 3.14 . **Left Column.** Interaction effects of suboptimal choice acquisition and delay discounting k values as a function of BELT losses per trial (first row) and with AUC values (second row). Interaction effects of suboptimal choice acquisition and delay discounting k values as a function of BART CV (third row) and with AUC values (fourth row). **Right Column.** Predicted values of suboptimal choice acquisition as a function of mean centered BELT losses at low, medium, and high k values (first row), AUC values (second row), and as a function of BART CV at low, medium, and high k values (third row) and AUC values (fourth row).

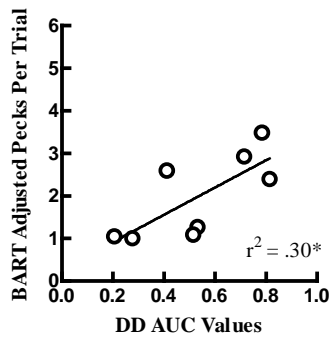
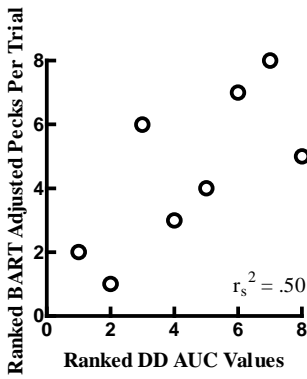
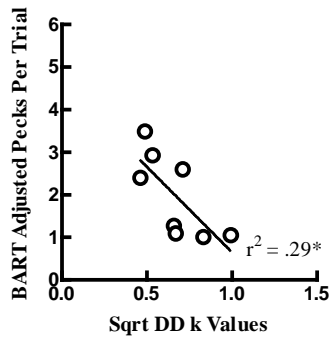
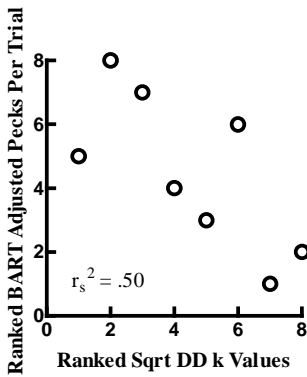
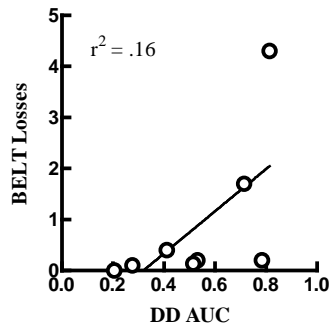
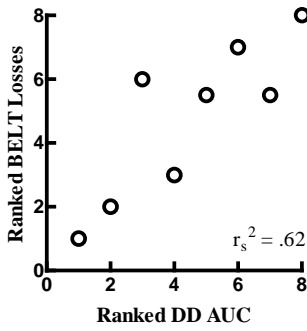
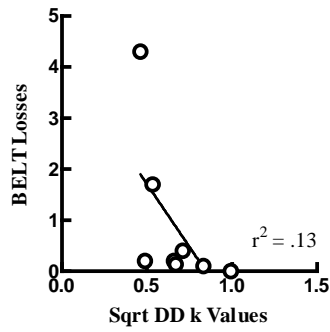
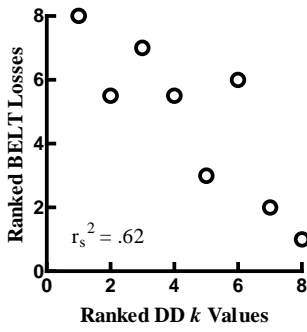


Figure 3.15. Left Column. Changes in significant Spearman ranked correlations primary task variables in Experiment 2 after outliers were removed. **Right Column.** Pearson correlations with regression line of best fit between significantly changed Spearman correlations after removing outliers. *Note: * indicates $p \leq .05$.*

Section IV: General Discussion

The purpose of the present studies was to examine a translated version of the balloon analogue risk task in pigeons to assess risk taking propensity. It was predicted that this task would show predictive validity similar to the human research with another risky choice task, the suboptimal choice task, and be separate from yet related to constructs such as impulsivity. These hypotheses were examined through using the balloon emotional learning task as an index of the pigeons' ability to discriminate the task contingencies when risk levels were relatively low (Humphreys et al., 2013), a delay discounting task to assess impulsivity levels (Odum, 2011; Reynolds, 2006), and the suboptimal choice task that has been posited as an analogue of human gambling behaviors (Zentall, 2011).

In Experiment 1 we looked at these relationships using a non-signalized BELT task. Performance on this task was relatively poor (suboptimal) in that pigeons did not maximize reward similar to rats (Jentsch et al., 2010) even in low risk conditions. Despite this, more pecks per trial, pellets earned, and losses were associated with faster acquisition of the suboptimal choice task, substantiating the predicted hypotheses. Although impulsivity failed to relate directly to either the BELT or suboptimal choice tasks, there was evidence of moderation. Generally, greater discounting amplified these associations such that higher scores on primary BELT variables of pecks per trial and losses, in conjunction with greater discounting, were related to faster acquisition than when discounting was low. Conversely, lower scores on primary BELT variables in conjunction with greater discounting showed slower acquisition. These results seem best explained as the pigeons that were more sensitive to the greater magnitudes of reinforcement in the BELT task also may have been more sensitive to the conditioned reinforcers associated with the suboptimal choice task.

Additionally, impulsivity seemed to exhibit more than one possible effect, as pigeons high in impulsivity could be both high or low responders on the BELT task and changed the speed of acquisition.

Experiment 2 used a similar design but signaled the number of pecks made through a different colored stimulus for each peck. Results indicated that performance was sufficiently improved to assess performance under conditions of high risk in the BART task. Again supporting the predicted hypotheses, greater losses in the BELT task were significantly associated with greater BART pecks per trial, variability in responding, and losses. Greater discounting showed positive correlations with BELT (with outliers) and BART variability (with and without outliers) as well as negative correlations with BELT losses (without outliers), BART pecks per trial (with and without outliers), and adjusted pecks (without outliers).

BELT losses and BART variability also had significant correlations with slower suboptimal choice acquisition and, while impulsivity had no direct association with suboptimal choice, again showed evidence of moderating these relationships. The moderation in Experiment 2, though, amplified the effects only when both BELT losses and BART variability were high, showing slower learning in conjunction with greater discounting levels with little effect when BELT losses and BART variability were low. These results, similar to Experiment 1, also seemed best explained from a discriminability framework, but appear to show a lack of discriminability. As the BELT task in Experiment 2 was signaled, this increased the potential to respond optimally without large amounts of losses, yet those that experienced greater amounts of losses may not have been as sensitive to when to stop responding. Similarly, greater variability in the BART task may imply that

these pigeons had a lack of controlled choice behavior (Jentsch et al., 2010) and were less able to exploit a strategy in both BART task.

The results of both experiments seem to suggest the performance on the BELT, BART, and suboptimal choice tasks may result from similar mechanisms. Recent research has posited that the suboptimal choice task results both from a decreased sensitivity to losses (Laude, Stagner, et al., 2014) as well as a heightened sensitivity to conditioned reinforcers with either greater predictive validity of food (Stagner & Zentall, 2010; Zentall et al., 2015) or that signal greater magnitudes of food (Zentall & Stagner, 2011), similar to humans (van Holst et al., 2010). The present research found congruent results in that the pigeons showed no difference in the average number of pecks following a win or loss in either the BELT or BART tasks, resulting in little influence on local fluctuations in behavior. The pigeons did as a group, however, show a significant decrease in the number of pecks per trial between the BELT and BART tasks in Experiment 2. It is difficult to distinguish, though, between how much of this decrease may be due to losing at higher values of pecks versus choosing to cash out earlier, as both number of pecks and adjusted pecks were very similar.

Additionally, greater amounts of BELT pecking in Experiment 1 likely occurred due to sensitivity to the increased magnitudes of reinforcement. This is analogous to pigeons preferring stimuli that predict greater magnitudes of food in the suboptimal choice task (Zentall & Stagner, 2011). Alternatively, Experiment 2 provided a signal for the number of pecks and reinforcers. This had the effect providing distinctive conditioned reinforcers that predicted the increasing magnitude of reinforcement (up to 5 pellets). That 5-pellet stimulus became the preferred stimulus similar to the pigeons' preference in the suboptimal choice tasks involving stimuli that predict different probabilities of reinforcement (Stagner &

Zentall, 2010; Zentall et al., 2015). Once sufficient experience allowed for learning of the different conditioned reinforcers, choice tended to shift towards preferring the conditioned reinforcers associated with greater magnitudes of reinforcement. Thus, performance on the BELT and BART tasks may be based on a similar mechanism of sensitivity to conditioned reinforcers and magnitudes of reinforcement in conjunction with decreased sensitivity to losses, similar to the suboptimal choice task.

The role of impulsivity in these tasks, however, is not as straightforward. Research with the BART task in humans has shown that, when associations are found, impulsivity is associated with increased responding (Lejuez, Aklin, Zvolensky, et al., 2003; Lejuez et al., 2002; Vigil-Colet, 2007). Experiment 1 found no direct association between impulsivity and the unsigned BELT task (possibly due to the restricted range in the pigeons' responding); however, the interaction predicting suboptimal choice acquisition when including impulsivity suggested that it is involved. In Experiment 1, high levels of discounting were associated with slower suboptimal choice acquisition when BELT adjusted pecks per trial and pellets earned were low, but faster when these levels were high. Additionally, BELT losses showed an amplified effect with high discounting that was associated with generally slower acquisition. This seems to suggest that impulsivity does not have a single, unitary effect on the BELT task. That is, some animals high in impulsivity may be attracted to the lower ordered cash out key conditioned reinforcer, pecking the add key only once or twice prior to ending the trial, while other pigeons may have shown behavior similar to the human experiments of pecking a greater number of times.

Alternatively, Experiment 2 found direct associations between delay discounting and the BELT and BART tasks. These correlations showed that high discounting was related to

greater BELT variability (with outliers) or fewer BELT losses (without outliers), showing an inverse association to that of Experiment 1. Additionally, higher discounting was also associated with fewer BART pecks, adjusted pecks per trial (without outliers), and losses. As variability and losses showed no association in performance of the BELT task, this may suggest that greater discounting in the signaled BELT task was associated with moderate levels of responding. That is, as responding is necessarily restricted when there is exclusive responding only 1 or 5 times prior to cashing out, responding is most variable at the middle values (i.e., 2-4 pecks per trial). This may also suggest that these pigeons were less consistent and did not tend to exploit a particular strategy.

When under conditions of high risk in the BART, however, greater discounting was associated with fewer pecks per trial and losses. The reason why this was not similar to the BELT task is unclear, however. One possibility is that more impulsive animals may indeed be influenced to peck less in the BELT task, through either delay of gratification or sensitivity to the cash out key, but the higher magnitude of rewards offsets this. In the BART, however, greater magnitudes become more infrequent. This may potentially either reduce their associative value relative to the incentive to cash out early or possibly reduce their conditioned incentive value due their infrequency. The interactions of impulsivity on BELT/BART task variables when predicting suboptimal choice may further suggest this account as impulsive animals may be less consistent in their response strategies, resulting in fewer pecks in the BELT/BART and slower suboptimal choice acquisition. These findings contrast the human research, however, with only one study showing a nonsignificant trend in that direction (Xu et al., 2013), revealing the need for further research to determine the cause of this incongruence.

Current prominent theories of impulsivity, however, may be congruent with these findings. For example, Killeen (2011) proposed that a primary mechanism involved in discounting is a loss of association between the response that produced a reinforcer over time. The present experiment could be accounted for by this memory model as the increased variability seen might suggest that a lack of exploiting any particular strategy is due to misremembering which stimuli led to which outcomes. Additionally, if the conditioned stimuli associated with greater reward magnitude do not gain sufficient conditioning, this may explain why these pigeons decreased responding under the high risk BART conditions because of an insufficient incentive to keep responding.

An alternative interpretation may take into account temporal information within this task. For example, learning that certain stimuli pay off with greater magnitudes of reinforcement, even at the cost of higher losses in the BART, requires accumulating the probabilities with which outcomes occur. However, animals that are impulsive may have shorter time horizons (Krebs & Kacelnik, 1984) and experience difficulty in keeping track of this information. A similar conceptualization has been posited by recent research with rats. This line of research found that high rates of discounting tended to positively correlated with both poorer temporal precision (Marshall, Smith, & Kirkpatrick, 2014; McClure, Podos, & Richardson, 2014; Smith, Marshall, & Kirkpatrick, 2015) and delay tolerances (Marshall et al., 2014), potentially showing an aversion to delays or an inability to delay gratification due to an inaccurate estimation of time. Together, these conceptually similar ideas may support the findings of impulsive animals having generally poorer discriminability among the various tasks, although the mechanisms by which this occurs is beyond the scope of this paper.

The primary difficulty in these interpretations, however, comes from the discordant results from the study by Laude, Beckmann, et al. (2014), which showed greater discounting was associated with higher asymptotic levels of suboptimal choice. In their study, the less impulsive animals did not seem to acquire a strong preference for the suboptimal alternative, with choice around 60% after 25 sessions of training. This further seems to suggest that acquisition among the less impulsive animals should be slowed. Both experiments in the present work showed all pigeons acquired a suboptimal preference relatively quickly, but these differences may highlight the importance of distinguishing between spatial versus visual discriminations when using pigeons in choice tasks. The expected pattern of higher impulsivity leading to faster acquisition was also not upheld, however, as Experiment 1 showed correlations inconsistent with this pattern while Experiment 2 only showed trends in the expected direction without outliers. These discrepancies clearly warrant further investigation into what common underlying process exists between the delay discounting task and each of these risky choice tasks.

In conclusion, the present set of experiments has shown that pigeons can serve as an effective model in the balloon analogue risk task. Significant associations were found between the BART, its low-risk variation, the BELT, a delay discounting task, and acquisition of a suboptimal choice task. Additionally, while impulsivity was related to the signaled BELT and BART tasks, only the BELT/BART was directly associated with suboptimal choice acquisition and suggests that impulsivity is a related but distinct construct from the BART. The present research was limited, however, primarily by its small sample size. Experiment 2 sought to remedy this through the inclusion of 10 birds but the performance of the hopper group did not reach that of the pellet group. The associations

shown in these experiments also appear to be complex, making it difficult to distinguish what results may be replicable due to both insufficient power to pick up higher order effects such as curvilinear relationships and possible effects being overly driven by few data points.

Despite these limitations, the present research has illustrated several relationships among these different risky choice tasks and an unrelated delay discounting tasks, demonstrating a fruitful area of future research to further examine the mechanisms underlying risk taking behavior across different contexts.

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