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MECHANISMS OF IMPULSIVE CHOICE: I. INDIVIDUAL DIFFERENCES IN INTERVAL TIMING AND REWARD PROCESSING

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Impulsive choice behavior incorporates the psychological mechanisms involved in the processing of the anticipated magnitude and delay until reward. The goal of the present experiment was to determine whether individual differences in such processes related to individual differences in impulsive choice behavior. Two groups of rats (Delay Group and Magnitude Group) were initially exposed to an impulsive choice task with choices between smaller–sooner (SS) and larger–later (LL) rewards. The Delay Group was subsequently exposed to a temporal discrimination task followed by a progressive interval task, whereas the Magnitude Group was exposed to a reward magnitude sensitivity task followed by a progressive ratio task. Intertask correlations revealed that the rats in the Delay Group that made more self-controlled (LL) choices also displayed lower standard deviations in the temporal bisection task and greater delay tolerance in the progressive interval task. Impulsive choice behavior in the Magnitude Group did not display any substantial correlations with the reward magnitude sensitivity and progressive ratio tasks. The results indicate the importance of core timing processes in impulsive choice behavior, and encourage further research examining the effects of changes in core timing processes on impulsive choice.

Key words: impulsive behavior, discounting, timing, reinforcer magnitude, rats

Impulsive choice has traditionally referred to the preference for a smaller–sooner (SS) outcome over a larger–later (LL) outcome. When preference for the LL is more optimal in terms of rewards earned per unit of time, impulsive choices are indicative of deficient decision making. Indeed, the tendency to make impulsive choices has been associated with several maladaptive behaviors and clinical disorders such as substance use and abuse (e.g., Bickel & Marsch, 2001), gambling (e.g., Reynolds, 2006), obesity (e.g., Bruce et al., 2011; Weller, Cook, Avsar, & Cox, 2008), attention deficit hyperactivity disorder (ADHD; Barkley, Edwards, Laneri, Fletcher, & Metevia, 2001; Bitsakou, Psychogiou, Thompson, & Sonuga-Barke, 2009; Marco et al., 2009), schizophrenia (Heerey, Robinson, McMahon, & Gold, 2007), depression (Imhoff, Harris, Weiser, & Reynolds, 2013), borderline personality disorder (Lawrence, Allen, & Chanen, 2010), and Parkinson's disease with a comorbidity of impulsive-compulsive behavior (Housden, O'Sullivan, Joyce, Lees, & Roiser, 2010).

In humans, individual differences in impulsive choice are relatively stable over time with test–retest reliability statistics in the range of other trait variables (Baker, Johnson, & Bickel, 2003; Jimura et al., 2011; Johnson, Bickel, & Baker, 2007; Kirby, 2009; Matusiewicz, Carter, Landes, & Yi, 2013; Ohmura, Takahashi, Kitamura, & Wehr, 2006; Peters & Büchel, 2009). Recent research in rats has also revealed stable individual differences in impulsive choice across testing conditions, suggesting that rats may also exhibit trait impulsivity (Galtress, Garcia, & Kirkpatrick, 2012; Garcia & Kirkpatrick, 2013). However, despite the clear importance of individual differences in impulsive choice in predicting a wide range of behavioral problems (e.g., MacKillop & Kahler, 2009; Perry & Carroll, 2008), the source of such individual differences remains poorly understood. Therefore, examining the underlying mechanisms that contribute to variability in impulsive choice will help elucidate the source of individual differences as well as identify the primary factor(s) driving impulsivity.

One possible source of the individual differences in impulsive choice is the core temporal processing mechanism involved in delay processing (Wittmann & Paulus, 2008). One such factor that could explain individual differences is poor *precision* in timing due to increased variance (noise) in timing processes (see Galtress et al., 2012; Smith, Marshall, & Kirkpatrick, 2014). An alternative possibility that has been suggested is that the tendency to make impulsive choices may

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be a direct result of subjective overestimation of the delay until reward delivery due to poor timing *accuracy* (McGuire & Kable, 2013; Wittmann & Paulus, 2008). A number of diseases and disorders that involve deficits in impulsive choice also demonstrate a comorbidity of disruptions in time processing (accuracy and/or precision), such as schizophrenia, ADHD, and substance abuse disorders (see Allman & Meck, 2011; Barkley et al., 2001; Bickel & Marsch, 2001; Heerey et al., 2007; Wittmann & Paulus, 2008).

Behavioral research examining the relationship between impulsive choice and timing in humans has also indicated that more impulsive individuals tend to overestimate interval durations (Baumann & Odum, 2012) and exhibit earlier start times on a fixed interval schedule (Darcheville, Rivière, & Wearden, 1992), suggesting that individual differences in impulsive choice in humans may be affected by corresponding individual differences in anticipatory time perception (Kim & Zauberman, 2009). Additionally, previous research has identified poor temporal discrimination capabilities in impulsive individuals (van den Broek, Bradshaw, & Szabadi, 1992), suggesting that these individuals exhibit reduced temporal precision relative to nonimpulsive controls. Finally, poor timing abilities have been linked to delay aversion (which is a predictor of impulsive choice). Delay aversion stems from the motivation to reduce the overall delay to reward due to the subjectively aversive nature of waiting during delays to reward (Sonuga-Barke, Taylor, Sembi, & Smith, 1992). Delay aversion may be related to overestimation of intervals and/or poor temporal precision, as individuals motivated to decrease overall delay may have reduced experience with longer durations due to opting for shorter delays; this reduced experience would then also predispose impulsive individuals with fewer opportunities to experience and learn longer temporal delays, potentially exaggerating the problem (see Galtress et al., 2012, for a relevant discussion).

Ballard and Knutson (2009) also reported that activity within the posterior parietal and dorsolateral prefrontal cortices, areas associated with temporal processing, was negatively correlated with both the delay to reward and increased levels of impulsivity (see Leon & Shadlen, 2003; Nenadic et al., 2003; Rao, Mayer, & Harrington, 2001). However, Baumann and Odum (2012) showed that impulsivity was not significantly correlated with the standard deviation of the psychophysical function from a temporal bisection task, suggesting that impulsive choice and temporal precision were unrelated. Thus, the combined behavioral and neurobiological evidence seem to indicate a potential relationship between timing processes and impulsive choice in humans, but further evidence is warranted.

Little research has, however, examined timing–choice relationships in rats, a popular preclinical model of impulsive choice behavior. To our knowledge, three studies have examined this relationship, demonstrating some indication of correlations between interval timing and impulsive choice. In two of these studies (Galtress et al., 2012; Heilbronner & Meck, 2013), the timing–choice relationship was measured within the impulsive choice task, and the correlations were not particularly robust. Galtress et al. suggested that the dynamics inherent in the choice procedure may reduce the ability to identify relationships between individual differences in interval timing and impulsive choice when measured within the same task. For example, if an individual rat selected the SS delay on most trials, then they would have little exposure to the LL delay, which could produce an inaccurate metric of that rat's LL timing behavior. More recently, McClure, Podos, and Richardson (2014) investigated the relationship between interval timing and impulsive choice in separate procedures, and found that the rats that timed with greater precision in a peak procedure were also those that made fewer impulsive choices. However, these authors posited that such a relationship may be more effectively studied by employing a temporal discrimination task to measure interval timing processes. Furthermore, another important factor related to timing processes is that impulsive choice behavior may be driven by an aversion to longer delays to reward (see Sonuga-Barke et al., 1992), which has been suggested as a key predictor of ADHD (see Bitsakou et al., 2009). Delay aversion could interact importantly with timing processes, as discussed above, and is a potentially important contributor to any timing-choice relationships. Therefore, the present experiment sought to determine the relationship between timing, delay aversion and choice behavior in rats by collecting measurements of core timing processes and delay aversion outside of the impulsive choice task.

A second cognitive process that is likely involved in impulsive choice is reward magnitude processing, and differential sensitivities to reward magnitudes may explain individual differences in impulsive choice (see Locey & Dallery, 2009). Consistent with this idea, several diseases and disorders that involve impulsive choice deficits also express comorbidities in reward processing deficits, such as ADHD and related impulse control disorders, substance abuse, and gambling (Ballard & Knutson, 2009; Bechara, Dolan, & Hindes, 2002; Cherniawsky & Holroyd, 2013; Cubillo, Halari, Smith, Taylor, & Rubia, 2012; Ripke et al., 2012; Verdejo-García, Lawrence, & Clark, 2008; Wilbertz et al., 2012). Furthermore, impulsive choice is correlated with activity in the ventral striatum/nucleus accumbens, posterior cingulate cortex, and medial prefrontal cortex (Andrews et al., 2011; Ballard & Knutson, 2009; Cooper, Kable, Kim, & Zauberman, 2013; Kable & Glimcher, 2007; Ripke et al., 2012; Sripada, Gonzalez, Luan Phan, & Liberzon, 2011; Verdejo-García et al., 2008). Activation in these brain areas is positively correlated with the subjective value of the LL reward (Ballard & Knutson, 2009; Kable & Glimcher, 2007; Ripke et al., 2012), and these regions are well-established components of the reward valuation circuit (e.g., Peters & Büchel, 2010, 2011). In addition, lesions of the orbitofrontal cortex (Mobini et al., 2002) and nucleus accumbens (Cardinal, Pennicott, Sugathapala, Robbins, & Everitt, 2001; Galtress & Kirkpatrick, 2010b) increase impulsive choice behavior in rats. Therefore, these findings support the relationship between reward magnitude processing, incentive motivation, and impulsive choice. Unfortunately, there have been relatively few direct observations of this relationship, particularly in rodent preclinical models (but see Locey & Dallery, 2009). Accordingly, the present study employed measures of reward magnitude sensitivity and incentive motivation to work for rewards of different magnitudes (i.e., elasticity/efficacy of reward) to determine potential relationships with impulsive choice behavior in rats.

The assessments of timing and reward magnitude processing were conducted in separate groups, as preliminary research in our laboratory has found carry-over effects from reward magnitude sensitivity testing that affected later assessment of temporal sensitivity (Galtress & Kirkpatrick, 2012), which is consistent with a recent report on carry-over effects when utilizing multiple tasks from different domains (Marusich, Darna, Charnigo, Dwoskin, & Bardo, 2011). The determination of a relationship between impulsive choice and timing and/or reward sensitivity would have considerable implications for the development of behavioral interventions targeting the psychological and neurobiological correlates of temporal and reward processing (see Smith et al., 2014).

Method

Subjects

Twenty-four experimentally-naïve male Sprague-Dawley rats (Charles River, Portage, MI) were used in the experiment. They arrived to the facility (Kansas State University, Manhattan, KS) at approximately 42–45 days of age. The rats were pair-housed within a colony room that was set to a 12-hr light:dark schedule (lights off at 6 pm). The rats were tested overnight during their dark phase. There was ad libitum access to water in their home cages and in the experimental chambers. The rats were maintained at approximately 85% of their projected ad libitum weight during the experiment based on growth curves obtained from the supplier. In addition to earning food pellets during the experiment, they were fed in their home cages following the experimental session.

Apparatus

The experiment was conducted in 24 operant chambers (Med Associates; St. Albans, VT) each housed within sound-attenuating, ventilated boxes ($74 \times 38 \times 60$ cm). Each chamber ($25 \times 30 \times 30$ cm) was equipped with a stainless steel grid floor, two stainless steel walls (front and back), and a transparent polycarbonate side wall, ceiling, and door. Two pellet dispensers (ENV-203), mounted on the outside of the operant chamber, delivered 45-mg food pellets (Bio-Serv; Frenchtown, NJ) to a food cup (ENV-200R7) centered on the lower section of the front wall. Head entries into the food magazine were transduced by an infrared photobeam (ENV-254). Two retractable levers (ENV-112CM) were located on opposite sides of the food cup. The chamber was also equipped with a house light (ENV-215) that was centered at the top of the front wall, as well as two nose-poke key

lights (ENV-119M-1) that were located above the levers. Water was continuously available from a sipper tube that protruded through the back wall. Experimental events were controlled and recorded with 2-ms resolution using MED-PC IV (Tatham & Zurn, 1989).

Procedure

The rats were randomly assigned to two groups ($n = 12$), the Delay Group and the Magnitude Group. All experimental sessions took place overnight, lasting for a maximum of 14 hr. Previous research in our laboratory using long sessions has resulted in stable and systematic choice behavior (Galtress et al., 2012; Galtress & Kirkpatrick, 2010b; Kirkpatrick, Marshall, Clarke, & Cain, 2013), which is ideal for collecting stable individual-differences measurements. The sessions were divided into blocks with interblock intervals imposed to attenuate satiety over the course of the long testing period.

Initial training. The initial training procedure involved one session of magazine training and lever-press training delivered in four blocks, each separated by a 30-min interblock interval (IBI); one rat required a second session of initial training. In Block 1 (magazine training), 30 food pellets were delivered on a random-time 60-s schedule. In Block 2, the rats were trained to press the left and right levers on a fixed ratio (FR) 1 schedule. The FR1 block was divided into four sub-blocks, in which the left or right lever was presented until 10 reinforcers were earned for pressing the corresponding lever. The FR1 block lasted until 20 reinforcers were delivered on each lever. A 10-min interval separated sub-blocks. In Block 3, a random ratio (RR) 3 schedule was delivered across four sub-blocks. During each sub-block, both levers were presented until five reinforcers were earned on each. The sub-blocks were separated by a 10-min interval, and the RR3 block continued until 20 reinforcers were earned on each lever. Block 4 involved an RR5 schedule, which was otherwise identical to the RR3 schedule.

Delay Group. The Delay Group received training on the impulsive choice task with variations in the delay to the SS outcome, followed by testing with a temporal bisection task and a progressive interval (PI) task.

Impulsive choice task. The impulsive choice task involved the delivery of four 50-trial blocks; there was a 30-min interval that occurred prior to the first block, and a 90-min IBI (Galtress et al., 2012; Garcia & Kirkpatrick, 2013; Kirkpatrick et al., 2013). Each block included 30 free choice (SS vs. LL), 8 SS forced, 8 LL forced, 2 SS peak, and 2 LL peak trials (see Roberts, 1981), delivered in a random order. The assignment of SS and LL outcomes to the left and right levers was counterbalanced across rats. On free-choice trials, both levers were inserted into the chamber; a lever press on one lever resulted in retraction of the other lever, illumination of the cue light above the chosen lever, and initiation of the corresponding delay. The first lever press on the chosen lever following the delay terminated the trial, and resulted in lever retraction, offset of the cue light, and food delivery. Forced choice trials were identical to free choice trials, except that only one lever was inserted. Peak trials were identical to forced choice trials, except that food was omitted, and the trial continued for 90 s, after which the corresponding lever was retracted and the cue light was turned off. There was a 120-s intertrial interval (ITI) that separated trials. Sessions lasted until all four blocks were completed, 240 reinforcers were delivered, or 14 hr had elapsed. The SS outcome was one pellet after a 30-, 10-, 5-, and 2.5-s delay in Phases 1-4, respectively, and the LL outcome was two pellets after a 30-s delay. Each phase lasted for 10 sessions. The final five sessions of Phases 2 and 4 were used for analysis. Due to an equipment error that resulted in the loss of data, sessions 4, 6, 7, 8, and 10 of Phase 1 and sessions 4, 5, 6, 8, and 10 of Phase 3 were used for analysis.

Temporal bisection task. The temporal bisection task was used to evaluate individual differences in temporal processing (e.g., Church & Deluty, 1977). Each session consisted of three blocks of trials, separated by a 90-min IBI, with a 30-min interval preceding the onset of the first block. During the training phase, the rats were trained to discriminate stimulus durations of a house light cue that lasted for 4 or 12 s, pseudorandomly alternated. Following house light offset, both levers were inserted into the chamber, corresponding to the "short" or "long" choices; the short and long levers were the same as the SS and LL levers, respectively, in the impulsive choice task. Following the rats' choice, both levers were retracted. If the rat made the correct choice, then one food pellet was delivered and a 15-s ITI began. If the rat made the incorrect choice, then correction trials

continued until the rat made the correct choice and reward was delivered; there was a 5-s ITI between an incorrect choice and the onset of a correction trial. Each training block lasted until 80 correct choices were made, with no limit on the number of correction trials. Training lasted for 5 days at which point the group mean of initial correct choices exceeded 80% for the preceding 2 days.

Subsequently, training and test sessions were intermixed, such that there was a training session following each set of three test sessions, with 12 total test sessions delivered. During the test sessions, the rats were exposed to a series of nonreinforced intermediate durations that were randomly intermixed with the training trials. Training trials were delivered in an identical manner as in the bisection training phase. An additional 14 test trials (without any correction trials) were presented within each of three blocks, for a total of 94 trials per block. These 14 test trials delivered two of each of the following durations: 4.00, 5.26, 6.04, 6.93, 7.94, 9.12, and 12.00 s. There was a 15-s ITI following test trials. Both training and test sessions lasted until the three blocks were completed or 14 hr had elapsed. The last 5 days of testing were used for data analysis.

PI task. A discrete-trial PI task evaluated the rats' subjective tolerance for increasingly longer delays to reward. The task was divided into four blocks with an 80-min IBI and a 30-min interval before the onset of the first block. Trial onset was cued by insertion of the left lever; the first response after the target delay had elapsed resulted in delivery of one food pellet, lever retraction, and the onset of a 30-s ITI. The target duration for the first trial was equal to the PI duration (e.g., 2.5 s), and this delay incremented arithmetically by the PI duration for each subsequent trial. The PI length was 2.5, 5, 10, and 30 s in Phases 1-4, respectively. If 10 min elapsed without a response on the left lever, then the lever retracted, the IBI began, and the PI interval length reset to the initial PI value for the subsequent block. The interval duration that had been most recently completed upon block termination was regarded as the breakpoint. Each session lasted until four blocks were completed, or 14 hr had elapsed. Phase 1 lasted for three sessions, and Phases 2-4 lasted for two sessions each. For the majority of the rats, the last day of each phase was used for analysis. Due to data loss, the second session of Phase 1 was used for analysis of one rat's data, and, the first session of Phase 4 was used for analysis of two rats' data. For all rats, only the completed blocks were used for data analysis.

Magnitude Group. The Magnitude Group received the impulsive choice task with variations in the LL magnitude followed by testing with the reward magnitude sensitivity task and the progressive ratio (PR) task.

Impulsive choice task. The impulsive choice task delivered to the Magnitude Group was identical to the task given to the Delay Group, with the exception that the SS was one pellet delivered after 10 s, and the LL was one, two, three, or four pellets delivered after 30 s in Phases 1-4, respectively.

Reward magnitude sensitivity task. The reward magnitude sensitivity task was used to evaluate individual differences in reward magnitude discrimination (Galtress & Kirkpatrick, 2010b; Kirkpatrick et al., 2013). The task was divided into three 80-trial blocks, with a 90-min IBI and a 30-min interval that occurred prior to the first block. On each trial, either the left or right lever was inserted into the chamber, with order pseudorandomly alternating. Presses on the lever were reinforced according to a random interval (RI) 30-s schedule; each interval was randomly drawn from an exponential distribution with a mean of 30 s. Trials were separated by a random-time 120-s ITI. Initially, both levers delivered one pellet on each trial. Following the baseline phase (Phase 1), the reward magnitude on one lever (i.e., the lever on which LL rewards had been arranged in the impulsive choice task) was increased to two, three, and four pellets in Phases 2-4, respectively. Each session lasted until all three blocks were completed, 240 reinforcers were delivered, or 14 hr had elapsed. Phase 1 lasted for 15 sessions to establish initial baseline performance and Phases 2-4 lasted for 5 sessions each. Response rates on the two levers across the last three sessions of each phase were used for data analysis.

PR task. A discrete-trials PR3 task was used to evaluate incentive motivation to work for different reward magnitudes, a measure of elasticity and efficacy of reward (Bickel, Marsch, & Carroll, 2000; Hodos, 1961). The task was divided into four blocks with an 80-min IBI and a 30-min interval prior to the first block. The left lever was inserted to initiate a trial, and an initial response requirement of three responses earned the first reinforcer. The response requirement increased

by three responses following each reinforcer earned. Following completion of the response requirement the trial terminated, resulting in food delivery, lever retraction, and onset of a 30-s ITI. If 10 min elapsed without a lever response, then the lever retracted, the IBI began, and the initial response requirement for the subsequent block was reset to three. The ratio requirement that had been most recently completed upon block termination was regarded as the break-point. Each session lasted until all four blocks were completed, or 14 hr had elapsed. In Phases 1-4 of the PR task, food reward was one, two, three, and four pellets, respectively. Phase 1 lasted for three sessions, and Phases 2-4 lasted for two sessions each. The last session of each phase and only the completed blocks within the session were used for data analysis.

Data Analysis

The approaches to deriving and analyzing specific measures within each task are discussed below. All summary measures were obtained from the raw data using MATLAB (The MathWorks, Natick, MA) and all statistical analyses were conducted in SPSS (IBM, Armonk, NY). The alpha value for significance testing was .05 and only the significant results are presented.

Results

Delay Group

Impulsive choice task. Figure 1 shows the individual rat (lines) and group mean (bars) log odds of LL choices as a function of SS delay. The log odds of LL choices is a more sensitive measure to detect individual differences in choice behavior as this measure reduces ceiling and floor effects imposed by percentage choice measures. Log odds also more readily meets the scaling assumptions of parametric analyses due to the removal of artificial restrictions (i.e., the 0–100 range of percentage measures) on variance in the data collected at different choice points. Accordingly, log odds was computed as the natural logarithm of the ratio of the number of LL choices to the number of SS choices. To account for exclusive choice for the SS or LL outcome, a value of 0.5 was added to both the numerator and denominator of the odds ratio (see Garcia & Kirkpatrick, 2013; Haldane, 1956). As the SS delay increased, the rats increased their choices for the LL outcome. However, there were considerable individual differences in choice behavior that were relatively stable across testing conditions, consistent with recent findings (Galtress et al., 2012; Garcia & Kirkpatrick, 2013). Specifically, reliability analyses indicated that the rats' choices demonstrated excellent consistency across phases, $\alpha = .91$, in accordance with criteria suggested previously (George & Mallery, 2003). A repeated-measures analysis of variance (ANOVA) revealed a significant effect of SS delay on LL choices, $F(3, 33) = 105.98$, $p < .001$, $\eta_p^2 = .91$.

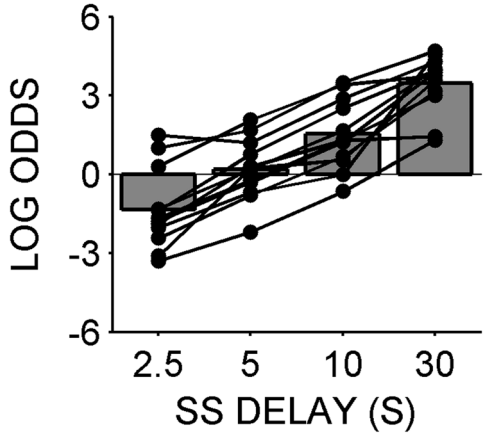

Fig. 1. Log odds of larger–later (LL) choices as a function of the smaller–sooner (SS) reward delay for the individual rats in the Delay Group (lines). The bars represent the group mean.

Temporal bisection task. Figure 2 shows the proportion of choices for the long lever as a function of the duration of the house light stimulus on nonreinforced test trials. As the stimulus duration increased, the number of long responses increased, $F(6, 66) = 100.46$, $p < .001$, $\eta_p^2 = .90$. There were considerable individual differences in the psychophysical functions that were consistent across stimulus durations, $\alpha = .73$. A cumulative logistic distribution was fitted to each rat's psychophysical function using MATLAB: $1/e^{-(x-\mu)/\sigma}$, in which x was the stimulus duration, μ was the mean of the function (an index of timing accuracy), and σ was the standard deviation of the function (an index of timing precision, or noise in timing). The logistic function provided good fits to the data, accounting for a mean of 96% of the variance. Table 1 shows the best-fitting parameters for each rat. One-sample t-tests revealed that the mean of the logistic function was not statistically different from the geometric mean of the

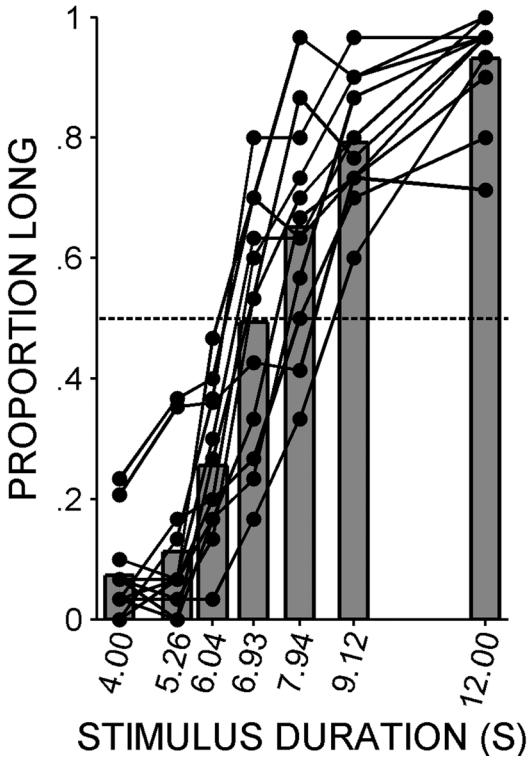

Fig. 2. Proportion of choices for the long lever as a function of stimulus duration for the individual rats in the Delay Group within the temporal bisection task (lines). The bars represent the group mean.

anchor durations of 4 s and 12 s (6.93 s), but did significantly differ from both the arithmetic (8 s), $t(11) = 3.35$, $p = .007$, and harmonic means (6 s), $t(11) = 5.68$, $p < .001$.

Table 1

Mean (μ) and standard deviation (σ) of the cumulative logistic functions fitted to the individual rat's psychophysical functions from the temporal bisection task (Fig. 2).

Rat	Mean (μ)	St. Dev. (σ)
1	7.7	0.8
2	7.0	1.2
3	6.4	2.3
4	7.9	3.3
5	6.9	0.8
6	8.2	1.6
7	6.9	0.7
8	7.2	0.9
9	8.7	1.1
10	6.3	0.6
11	6.3	0.6
12	7.6	1.0

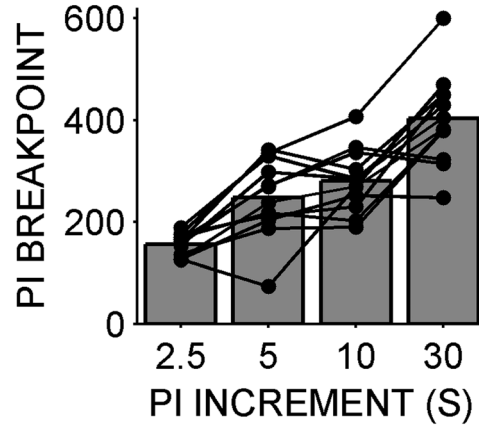

Fig. 3. Breakpoint in the progressive-interval (PI) task as a function of the size that the PI increments with each reinforcer delivery for the individual rats in the Delay Group (lines). The bars represent the group mean.

PI task. Figure 3 shows the breakpoint as a function of the PI increment. A later breakpoint is a measure of greater tolerance to increasingly longer delays to reinforcement. There was a significant increase in breakpoint as PI increment increased, $F(3, 33) = 42.08$, $p < .001$, $\eta_p^2 = .79$. There were also considerable and consistent individual differences across PI durations, $\alpha = .68$.

Intertask correlations. Bivariate correlational analyses were conducted to determine if individual differences in impulsive choice (Fig. 1) could be accounted for by individual differences in interval timing (Fig. 2) and delay tolerance (Fig. 3). From the impulsive choice task, the two measures entered into the correlational analysis were the mean log odds of LL choices across SS delays (a measure of bias in choice) and the slope of the log odds as a function of normalized SS delay (a measure of adaptability of choice behavior; scaled from 0 to 1, so that the predictor values were .08, .16, .33, and 1 for SS delays of 2.5, 5, 10, and 30 s, respectively). Specifically, the mean log odds of LL choices reflects bias, as a greater mean is indicative of a greater LL choice bias, in much the same way that greater area-under-the-curve values reflect more LL choices (Garcia & Kirkpatrick, 2013; Myerson, Green, & Warusawitharana, 2001). Furthermore, the slope of the function reflects sensitivity to manipulations of SS delay. Two temporal bisection measures (mean and standard deviation of the fitted logistic function) and one PI measure (mean breakpoint across all

PI increments) were correlated against the measures from the impulsive choice task. There were significant relationships between the mean log odds of LL choices and the standard deviation of the bisection function, $r = -.73$, $p = .007$. There was also a significant relationship between mean log odds of LL choices and mean breakpoint in the PI task, $r = .63$, $p = .028$ (Fig. 4). Finally, there was a significant relationship between the standard deviation of the bisection function and mean breakpoint in the PI task, $r = -.59$, $p = .045$.

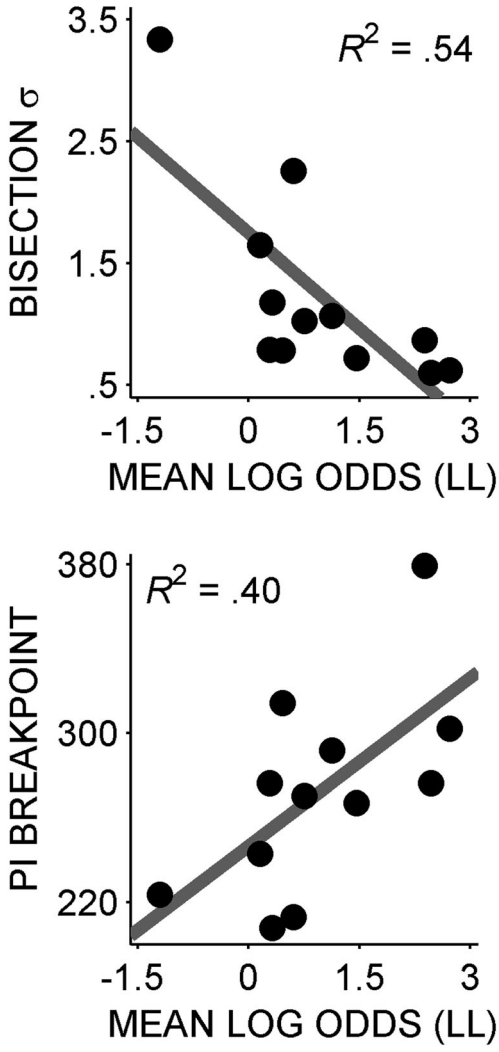

Fig. 4. Top panel: The individual rat's impulsive choice mean plotted against the standard deviation (σ) of the fitted logistic function of the individual's psychophysical functions from the temporal bisection task. Bottom panel: The individual rat's impulsive choice mean plotted against the mean breakpoint within the progressive-interval (PI) task. The variance accounted for by the best fitting regression line is shown (R^2).

Magnitude Group

Impulsive choice task. Figure 5 shows the log odds of LL choices as a function of LL reward magnitude. As reward magnitude increased, the rats significantly increased their choices for the LL outcome, $F(3, 33) = 115.09$, $p < .001$, $\eta_p^2 = .91$. Furthermore, there were considerable individual differences in choice behavior that were relatively stable across the different LL magnitudes, with good consistency across reward magnitudes, $\alpha = .86$.

Reward magnitude sensitivity task. Figure 6 shows the discrimination ratios (DRs) as a function of the large lever reward magnitude. The DRs were computed for each rat by dividing response rate on the large-reward lever by the sum of the rates on both levers. Response rate was calculated as the mean responses per min during the first 30 s of each trial, as the exponentially-distributed RI 30 s schedule included occasional very long intervals which can be accompanied by decreases in response rate over time. There were considerable individual differences in DRs that were consistent across all reward magnitude conditions, $\alpha = .80$, and all differential reward magnitude conditions (i.e., one pellet vs. two, three, or four pellets), $\alpha = .84$. There was a main effect of large lever reward magnitude on DRs, $F(3, 33) = 21.06$, $p < .001$,

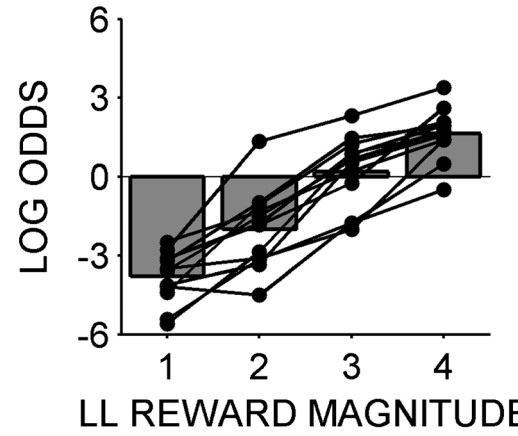

Fig. 5. Log odds of larger–later (LL) choices as a function of the larger–later (LL) reward magnitude for the individual rats in the Magnitude Group (lines). The bars represent the group mean.

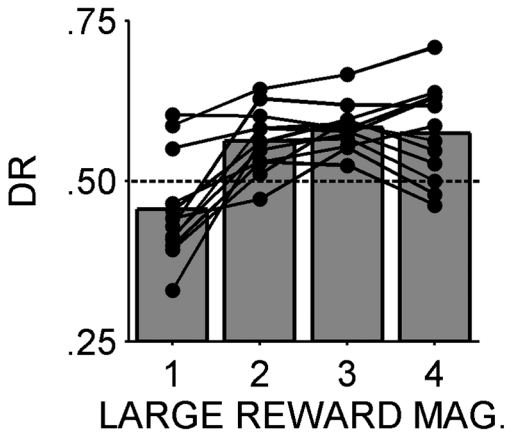

Fig. 6. Discrimination ratio (DR) between the large-lever and small-lever response rates as a function of the large-lever reward magnitude for the individual rats in the Magnitude Group (lines). The bars represent the group mean.

$\eta_p^2 = .66$; post-hoc tests with a Bonferroni correction revealed that this effect was due to significantly lower DRs when the large reward was one pellet, $ps < .05$ compared to the two, three, and four pellet phases. One-sample *t*-tests indicated that when the reward magnitude of both the small and large levers was equal to one pellet, the DR did not significantly differ from .50, but the DRs were significantly greater than .50 when the large lever resulted in two, three or four pellets, smallest $t(11) = 3.46$, $p = .005$.

PR task. Figure 7 shows the breakpoints as a function of reward magnitude. A higher breakpoint is indicative of greater incentive motivation to work for rewards of different magnitudes. There were considerable and consistent individual differences across reward magnitudes, $\alpha = .85$. There was a main effect of reward magnitude, $F(3, 33) = 14.82$, $p < .001$, $\eta_p^2 = .57$, which was due to a lower breakpoint when the PR reward magnitude was two pellets, $ps < .05$, compared to the other conditions, which did not differ.

Intertask correlations. Bivariate correlational analyses were conducted to determine if individual differences in impulsive choice (Fig. 5) were related to differences in reward magnitude sensitivity (Fig. 6) and incentive motivation (Fig. 7). Two impulsive choice measures (mean log odds of LL choices and the slope of this function over the LL magnitudes), two reward magnitude sensitivity measures (the mean DR across the two-, three-, and four-pellet large reward conditions; and the mean DR for the two to four pellet phases minus the DR in the one-pellet phase), and one PR measure (mean breakpoint across all reward magnitudes) were subjected to correlational analysis. For the choice function slope, the LL magnitudes were rescaled from 0 to 1 so that the predictor values were .25, .50, .75, and 1.00 for the magnitudes of one, two, three, and four pellets to produce comparable scaling to the Delay Group. The DR from the reward sensitivity test and PR breakpoint were significantly correlated, $r = -.72$, $p = .008$ (Fig. 8). There were no correlations between the reward sensitivity/

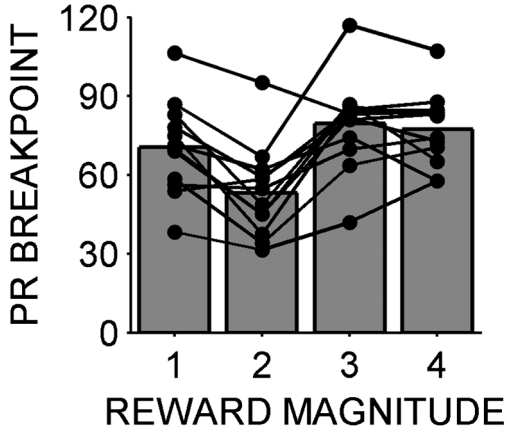

Fig. 7. Breakpoint in the progressive-ratio (PR) task as a function of the number of food pellets received with each reinforcer delivery for the individual rats in the Magnitude Group (lines). The bars represent the group mean.

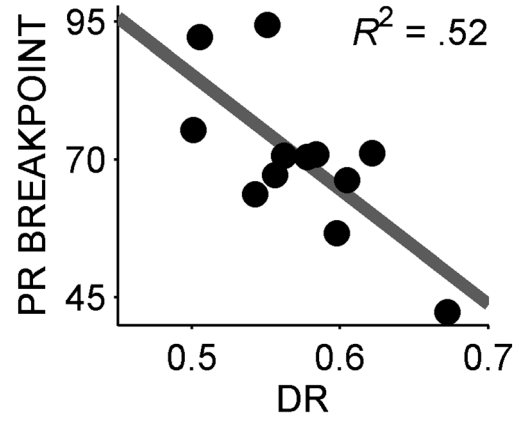

Fig. 8. The individual rat's discrimination ratio (DR) mean from the reward magnitude sensitivity task (the mean across the two-, three-, and four-pellet phases) plotted against the overall mean breakpoint in the progressive ratio (PR) task.

incentive motivation measures and either measure of impulsive choice.

Discussion

The present study sought to determine the underlying processes involved in impulsive choice by utilizing procedures designed to assess interval timing and delay aversion (Delay Group) as well as reward magnitude sensitivity and incentive motivation (Magnitude Group). The present interpretations of the results are specific to the set of tasks completed by each group. Specifically, holding reward magnitude constant in the Delay Group's impulsive choice task allowed for understanding the relationship between interval timing and impulsive choice, and the same was the case for the Magnitude Group. Given these task differences, a between-groups comparison of the correlational analyses conducted on the two groups is not attempted here. The primary aim of the present report was to determine the within-group timing- and reward-related correlates of impulsive choice, rather than to determine whether core timing mechanisms are more or less predictive than reward-related mechanisms of impulsive choice behavior. Accordingly, given the distinct patterns revealed by these assessments, the results produced by each group are discussed separately.

Impulsive Choice, Interval Timing, and Delay Aversion

The behavioral assessments of the Delay Group indicated that the mean log odds of LL choices (i.e., a measure of bias in impulsive choice behavior) was associated with imprecise timing and delay intolerance/aversion (Sonuga-Barke et al., 1992), as assessed through the standard deviation of the bisection psychophysical function and PI breakpoints, respectively. The present results corroborate a recent finding that rats exhibiting greater timing precision in a peak procedure also demonstrated greater self-control (McClure et al., 2014). Behavioral interventions designed to increase self-control by improving interval timing have also shown that temporal precision was primarily and more robustly affected via such manipulations, with little or no change in timing accuracy (Smith et al., 2014). Furthermore, in conjunction with previous research in humans (see Odum, 2011a, 2011b) and rats (Galtress et al., 2012), the individual differences observed in the corresponding procedures were relatively stable across conditions, suggesting that the psychological processes of impulsive choice, timing behavior, and delay aversion reflect underlying stable trait variables in rats. Ultimately, the present results demonstrate a clear relationship between core timing processes and impulsive choice, and suggest that timing processes may play a role in delay aversion (and/or vice versa), which could thereby drive impulsive choice behaviors. Therefore, future attempts to decrease impulsive behaviors should target and seek to improve the functioning of core timing processes through reductions in variability in timing (Smith et al., 2014).

The proposed relationship between interval timing mechanisms and impulsive choice behavior is not without precedent (e.g., McClure et al., 2014; McGuire & Kable, 2012, 2013; Rubia, Halari, Christakou, & Taylor, 2009; Wittmann & Paulus, 2008). Impulsive choice as a function of delay is well accounted for by a hyperbolic discounting function (e.g., Ainslie, 1975; Mazur, 1987), which has been proposed to occur as a result of a logarithmic representation of time (Cui, 2011; Gibbon, 1977; Han & Takahashi, 2012; Takahashi, 2005). Furthermore, it has been suggested that the tendency to make impulsive choices is due to an overestimation of the duration of a delay (Wittmann & Paulus, 2008). Baumann and Odum (2012) reported such a relationship, showing that humans who made more SS choices also exhibited shorter means of the psychophysical function within a temporal bisection task (i.e., they perceived interval durations as longer than those who more often chose LL rewards). They also showed a nonsignificant negative relationship between the tendency to make LL choices and the standard deviation of the bisection function, consistent with the significant negative correlations between the bisection standard deviation and the log odds of LL choices in the present experiment (Fig. 4). Therefore, in conjunction with previous research, the current results suggest that augmented levels of impulsivity may be governed by deficiencies in interval timing.

Because the present results are purely correlational, the direction of causality in the relationship between impulsive choice, timing, and delay tolerance remains to be determined.

There is some precedent for the suggestion that temporal precision may be a contributing factor in decisions between differentially delayed rewards (see Brunner, Gibbon, & Fairhurst, 1994; Gibbon, Church, Fairhurst, & Kacelnik, 1988). For example, greater temporal imprecision may be related to more suboptimal choice behavior in a time-left procedure (Gibbon & Church, 1981), in terms of rewards earned per unit of time (see Brunner et al., 1994). Indeed, with the current parameters, LL preference resulted in molar maximizing in all cases (see Flora & Pavlik, 1992), so the present results corroborate the previously proposed relationship between greater temporal imprecision and more suboptimal (impulsive) choices.

Alternatively, a second potential causal pathway driving impulsive choice behavior involves delay aversion as the primary factor, which could then produce secondary effects on interval timing. For example, Kim and Zauberman (2009) reported a significant positive relationship between human individuals' subjective discounting rates of delayed rewards and their diminishing sensitivities to increasing delays, which may be comparable to a decreased delay tolerance in the current PI task. Delay aversion has also been identified as a key behavioral trait of individuals with ADHD in relation to impulsive choice behavior (Bitsakou et al., 2009; Marco et al., 2009; Solanto et al., 2001), and has been suggested to be the explanatory factor producing an avoidance of long LL delays and preference for shorter SS delays (i.e., the delay aversion hypothesis; see Sonuga-Barke et al., 1992). The rats in the present experiment that were more tolerant of longer delays to reward in the PI task were also those that made more self-controlled (LL) choices (Fig. 4). Furthermore, individuals with ADHD have also been shown to exhibit deficits in temporal precision in a temporal bisection task (Suarez, Lopera, Pineda, & Casini, 2013). Therefore, if the dual impairment in temporal sensitivity and impulsive decision making were caused by inherent tendencies to avoid aversively long delays to reward, then delay aversion/tolerance may reflect the primary mechanism governing decisions between differentially delayed and sized rewards.

The promotion of self-control due to decreases in variance in timing in rats suggests that core timing processes play a causal role in impulsive choice (Smith et al., 2014), but it is additionally possible that delay aversion is a second causal pathway, and it may be the case that timing processes and delay aversion interact to produce impulsive choice. Alternatively, the individuals' behavior across tasks may reflect the influence of another underlying mechanism that collectively affects the corresponding task performances. For instance, differential attentional capacities and subjective attention to time have been employed to explain behavior in interval timing and impulsive choice tasks (see Ebert & Prelec, 2007; Fortin, 2003; Fortin & Massé, 2000; Galtress & Kirkpatrick, 2010a; Zauberman, Kim, Malkoc, & Bettman, 2009). Therefore, further research should attempt to pinpoint the role of these two different processes in impulsive choice behavior.

In contrast to the strong correlations between the secondary task measures and mean LL choices, there were no significant relationships with the slope of the log odds of LL choices function. This may have been at least partially due to the relatively small individual variability in the slopes of the impulsive choice function (see Fig. 1). Alternatively, sensitivity to the changes in delay to reward may reflect a different psychological mechanism from those of delay aversion and temporal precision that may require testing with additional procedures. The slope of the impulsive choice function is a measure of adaptability in choice behavior, so it is possible that metrics of behavioral flexibility would correlate with the slope measure. Second, there were no significant correlations between the mean of the temporal bisection function and the two measures of impulsive choice. These results seemingly reflect independence between mechanisms of impulsivity and temporal accuracy, which is inconsistent with previous human research demonstrating a relationship between impulsive choice and over- versus under-estimations of temporal intervals (e.g., Wittmann & Paulus, 2008). However, these discrepancies may be partially explained by task demands and/or species differences. Indeed, a recent study investigating the relationship between impulsive choice and interval timing showed that rats that were more impulsive also exhibited poorer temporal precision in a peak procedure task; importantly, this study failed to identify a relationship between temporal accuracy and impulsive choice (McClure et al., 2014). Given the ecological validity of animal models of choice behavior (see

Kalenscher & van Wingerden, 2011), impulsive decision making may actually be driven by how well individuals subjectively discriminate different delays to reward rather than how well they track the objective durations of such intervals. Alternatively, the relationship between temporal precision and impulsive choice may be mediated by some third factor (McClure et al.), such as delay aversion or attention to time (as described above). However, the small sample size of the present experiment inhibits our ability to detect a potentially significant mediation of delay aversion (see Fritz & MacKinnon, 2007). Thus, future research should continue investigating the direct and mediated relationships between interval timing, delay aversion, and impulsive choice behavior.

Impulsive Choice, Reward Magnitude Sensitivity, and Incentive Motivation

Despite the significant effect of reward magnitude on impulsive choice behavior (Fig. 5), the rats' behavior in the reward magnitude sensitivity and incentive motivation (PR) tasks did not correlate with either the mean or slope measures of impulsive choice. However, there was a significant relationship between PR breakpoint and mean DR in the reward magnitude sensitivity task. Specifically, higher DRs in the reward magnitude sensitivity task were associated with lower mean breakpoints in the PR task. This relationship suggests that there is a shared mechanism in the two secondary tasks that may have been due to individual differences in incentive motivational processes. For example, DRs often increase over an experimental session (McSweeney, Weatherly, & Swindell, 1996), whereas incentive motivation often decreases across an experimental session with increases in satiation (cf., Killeen, 1995), suggesting that reward magnitude discriminability may be related to more moderate levels of incentive motivation. Alternatively, incentive motivation may affect how selectively the rat responds; that is, the rats with more moderate incentive motivational level may be more selective in their responding, potentially demonstrating greater responding for the larger reward in comparison to the small reward.

The lack of correlation between behaviors within the reward magnitude sensitivity, PR, and impulsive choice tasks is unexpected given that previous research has demonstrated that activity within brain regions associated with incentive motivation and reward valuation is related to behavior within impulsive choice tasks (see Ballard & Knutson, 2009; Kable & Glimcher, 2007; Ripke et al., 2012). In addition, lesions of reward-valuation brain regions have been shown to affect impulsive choice behavior in rats (e.g., Cardinal et al., 2001), and these effects have been linked to deficits in reward magnitude sensitivity (Galtress & Kirkpatrick, 2010b). Thus, it seems likely that reward magnitude sensitivity should contribute to individual differences in impulsive choice behavior. One possible source of the lack of correlation between impulsive choice and the secondary reward tasks used here is that relative response rate may be a poor measure of reward magnitude sensitivity (cf., Bonem & Crossman, 1988). For example, Catania and Sagvolden (1980) reported that pigeons' initial-link choice preferences in a concurrent-chains paradigm were unrelated to their response rates in the terminal links. Furthermore, in an impulsive-choice paradigm that manipulated reward magnitude, Galtress et al. (2012) showed that impulsive choice did not correlate with peak-trial response rate, suggesting a possible independence between the rate of responding for rewards and the choice between rewards.

An additional possible issue may reflect the difference in task structure. In the impulsive choice task, the rats were able to choose the magnitudes that they received, whereas in the reward magnitude sensitivity and PR tasks, the magnitudes were determined by the experimental conditions. Previous research suggests that choice is more sensitive to differences in reward magnitude relative to single-operant nonchoice arrangements, such as in the two secondary reward tasks employed here (see Bonem & Crossman, 1988, for a review). The present results corroborate this notion, as the two secondary tasks revealed stable individual differences in sensitivity to reward magnitude, and the tasks were correlated with each other, even though there was no correlation with impulsive choice. Thus, it seems plausible that the mechanisms driving behavior in tasks involving experimenter-controlled reward magnitude exposure are distinct from those driving behavior in tasks involving subject-controlled reward magnitude exposure (i.e., impulsive choice tasks). Therefore, to better understand how individual differences in reward processing contribute to individual differences in impulsive

choice behavior, subsequent research should consider other methods to evaluate reward magnitude sensitivity, such as concurrent schedules of reinforcement.

An additional factor that may have contributed to the poor correlation between choice and other reward measures is the order of delivery of the parameters of the impulsive choice task. All of the rats received the same sequence of delivery of the magnitudes within the impulsive choice task, which was an ascending sequence. Previous work using a progressive interval versus fixed interval choice task demonstrated that an ascending sequence of magnitudes produced more optimal choice behavior (in terms of molar maximizing) than a descending sequence of magnitudes (Galtress et al., 2012), which is the reason for selection of this sequence for use in the present study. In addition, in their experiments, the individual-differences correlations between timing within the choice task and choice behavior were positive with the ascending sequence and negative with the descending sequence. This suggests that testing order may play an important role in affecting individual differences, a factor that clearly requires further study. The present study also did not counterbalance the order of delivery of the choice tasks and the secondary tasks which may have affected the results. The choice task was delivered first to minimize any contamination of choice behavior by prior exposure to the rewards (or delays), which has been shown to alter choice behavior in children (e.g., Eisenberger & Adornetto, 1986). However, it is possible that exposure to the choice task may have contaminated our secondary task measurements. If so, then a different approach will be needed to assess individual differences in reward processing and choice behavior in future research.

Conclusions

Individual differences in behavioral measures has become an increasingly critical topic for psychological study (Harzem, 1984; Odum, 2011a, 2011b; Odum & Baumann, 2010), and impulsivity is a particularly important individual difference variable given its relationship with a variety of other behavioral problems (see de Wit, 2008; Evenden, 1999; Perry & Carroll, 2008). The present experiment demonstrated that individual differences in temporal precision and delay tolerance can account for substantial variance (~50%) in individual differences in impulsive choice. As there have been relatively few empirical analyses regarding the relationship between interval timing and impulsive choice in nonhuman animals, the present results provide an important and novel contribution to the literature. Specifically, the results suggest that individual differences in temporal precision and delay tolerance serve as critical predictors of an individual's impulsive choices. The results are consistent with the suggestion by Kim and Zauberman (2009) that individual differences in factors related to impulsive choice such as substance abuse (e.g., Bickel & Marsch, 2001), age (e.g., Green, Fry, & Myerson, 1994), income (e.g., Green, Myerson, Lichtman, Rosen, & Fry, 1996), and intelligence (e.g., Shamosh & Gray, 2008), may be parsimoniously accounted for by differences in time perception. The current results unveil a potential avenue for the development of both rapid screening techniques and intervention protocols to address deficient impulsive decision making tendencies via the targeting of timing-related mechanisms (Smith et al., 2014).

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