Kathryn L. Humphreys[1,2]
Steve S. Lee[1]
Eva H. Telzer[3]
Laurel J. Gabard-Durnam[1,5]
Bonnie Goff[1]
Jessica Flannery[4]
Nim Tottenham[1,5]

[1]Department of Psychology
University of California
Los Angeles, CA

[2]Department of Psychiatry and Behavioral
Sciences
Tulane University School of Medicine
New Orleans, LA

[3]Department of Psychology
University of Illinois
Urbana-Champaign, IL

[4]Department of Psychology
University of Oregon
Eugene, OR

[5]Department of Psychology
Columbia University
New York, NY
E-mail: Nlt7@columbia.edu

Exploration—Exploitation Strategy is Dependent on Early Experience

ABSTRACT: *Traditional conceptualizations of early adversity characterize behavioral outcomes as maladaptive. However, conditional adaptation theory proposes that differing behavioral phenotypes following early experience are appropriate for the expected environment (e.g., behaviors likely to result in the best outcome based on environmental expectations). In the present study, youth with (n = 46) and without (n = 91) a history of previous institutionalization completed a laboratory-based experimental paradigm in which exploration—exploitation strategy was examined, a phenotype relevant to environmental expectations. Previous institutionalization was associated with decreased exploration and increased exploitation. A strategy favoring exploration resulted in greater success in the generous task condition whereas a strategy favoring exploitation produced greater success in the restricted task condition. These results suggest that exploration—exploitation strategy may be influenced by early experience, and the resulting success of strategy choice is context dependent and in line with expectations of the future environment based on early experience.* © 2015 Wiley Periodicals, Inc. Dev Psychobiol. :313–321, 2015.

Keywords: previous institutionalization; exploration; exploitation; separation anxiety; conditional adaptation

INTRODUCTION

Exploration—Exploitation Strategy is Dependent on Early Experience

The potential benefits of exploration (i.e., the probing of options with unknown and potentially rewarding or punishing outcomes) versus exploitation (i.e., selecting a limited but reward-promising outcome) are context dependent, with no optimal strategy in unknown environments (Cohen, McClure, & Yu, 2007). Under

conditions of relative safety, exploration allows for greater learning opportunities, whereas under conditions of threat, exploration may incur costs (see Lima & Dill, 1990). Similarly, exploitation will result in a safe outcome, but does not allow for additional information to be obtained. Decisions regarding exploration and exploitation are guided in part by contemporary context (e.g., the success of the last exploration attempt). In the current paper, we argue that decisions for exploration and exploitation are also influenced by developmental context, such that past experience guides strategy choice. For example, rats exposed to early adversity were found to be less exploratory relative to comparison rats (Spivey, Barrett, Padilla, & Gonzalez-Lima, 2008), perhaps because these adverse experiences occur during periods of rapid brain development in early life.

Traditional conceptualizations of early adversity focus on maladaptive outcomes (Cicchetti & Rogosch, 2001; Shonkoff & Garner, 2012), including heightened anxiety and attention to threat (Goff et al., 2012;

Shackman, Shackman, & Pollak, 2007). This focus is well-motivated given that early adversity can result in mental health difficulties later in life. Yet, in certain contexts, these biases may serve adaptive strategies. Though anxiety is often conceptualized as maladaptive, evolutionary theorists consider fear and anxiety as functional aspects of mammalian evolution (Öhman, 2000). Indeed, anxiety has been linked to increased exploitation of information for food acquisition in mice (Luksys, Gerstner, & Sandi, 2009), and anxiety predicts low-risk, low-reward decision-making under risk in humans (Raghunathan & Pham, 1999). Thus, it may be that individuals who are high in anxiety may fare best in contexts optimized for exploitation over exploration (see Prevention focused approaches; Crowe & Higgins, 1997; Higgins, 1998). During childhood, one of the most common forms of anxiety following institutional caregiving (i.e., orphanage rearing) is separation anxiety (Elliott & McMahon, 2011; Tottenham et al., 2011). While anxiety disorders are generally found to interfere with daily functioning (Henning, Turk, Mennin, Fresco, & Heimberg, 2007), anxiety may confer advantages during risky decision-making when conditions are optimized for exploitative decisions. In the current study, we considered how separation anxiety in PI youth might explain exploration versus exploitation biases, given that this behavioral phenotype may be conditionally adaptive following institutional care.

Conditional adaptation theory postulates that individuals develop tendencies that enhance the likelihood of survival and reproductive success based on their environment (Boyce & Ellis, 2005). As such, stress during ontogenetic development (without direct regard to evolutionary pressures) is theorized to influence behavioral tendencies. The current study sought to examine whether early adversity, in the form of previous institutionalization, was associated with exploration—exploitation strategy, a likely candidate for observing ontogenic adaptation to harsh versus supportive environments. Initial support for this approach is suggested by evidence of reduced risk-taking, a form of exploration, among previously institutionalized (PI) children (Loman, Johnson, Quevedo, Lafavor, & Gunnar, 2014). Recently, both individual differences (Zou, Scholer, & Higgins, 2014) and stress manipulations (Glass et al., 2011) have been used to better understand decision-making in relation to exploration and exploitation.

We experimentally tested exploration—exploitation strategy choice on a risky decision-making task (Humphreys, Lee, & Tottenham, 2013), modified from the Balloon Analogue Risk Task (BART; Lejuez et al., 2002), designed to provide different conditions in which exploration and exploitation strategy may be differentially related to success on the task. Previously, behavior on the BART was found to vary as a function of previous institutionalization (Loman et al., 2014), a potent stressor for the developing human (Gunnar, Bruce, & Grotevant, 2000; Tottenham, 2013). In the present study, the decision-making context was manipulated to create conditions optimized for either exploration (continue pumping for potentially larger gains) or exploitation ("cash in" early for a certain, but potentially smaller gain). The primary aim of the study was to examine: (1) to what extent previous institutionalization was associated with exploration and exploitation, and (2) how exploitation strategies operated in different contingency contexts. As behavioral phenotypes following early experience may be adaptive under certain contexts, we also examined to what extent separation anxiety, often found at elevated levels following previous institutionalization (Elliott & McMahon, 2011; Tottenham et al., 2011), mediated the association between early experience and exploitation.

METHOD

Participants

One hundred forty-three youth (83 girls, 60 boys, $M_{age} = 10.10$ years, $SD = 2.77$, age range: 6–15 years) were included from an ongoing longitudinal study. Participants included youth who experienced institutional care followed by adoption by families in the United States ($n = 49$) and comparison youth who had always lived with their biologically related parents and were never institutionalized ($n = 94$). Six participants (three PI, three comparison) were excluded due to invalid responses as noted by test administrators. Sample size was not pre-determined because this was a new task on a new population. Recruitment occurred continuously until a two-year period had elapsed from the start of the study, at which time data collection for this task ended. Table 1 includes the demographic information for all included participants ($N = 137$). Comparison participants were required to be free of serious medical illness, including head trauma, seizure disorder, and have IQs >70. Both children in the PI and comparison group had estimated IQs in the normal range as measured by the Wechsler Abbreviated Scale of Intelligence (Wechsler, 1999). The median income of families in both groups had an average household income above the median annual household income in the United States ($49,777; U.S. Census Bureau, 2012). The protocol was approved by the Institutional Review Board at the University of California, Los Angeles.

Table 1. Participant Demographics

	PI ($n = 46$)	Comparison ($n = 91$)
Age	10.32 (2.64) Range: 6.18–15.71	9.99 (2.84) Range: 6.00–15.93
Sex (% Male)	28%	47%
Median Family Income	$100,001–$150,000	$70,001–$85,000
Estimated IQ	105.19 (15.30)	110.88 (17.22)
Separation Anxiety	5.08 (3.48)	3.16 (3.27)
Psychotropic Medication (% yes)	20%	2%
Country of Origin	Belarus (1) China (17) Guatemala (1) Hungary (1) Indian (1) Kazakhstan (7) Russia (13) South Korea (2) Taiwan (1)	
Age placed in institution (months)	7.01 (15.29) Range: 0.00–72.00	
Age adopted (months)	24.18 (27.99) Range: 0.13–120.00	
Length of institutionalization (months)	16.98 (15.00) Range: 0.13–72.00	

Means (SD). PI, previously-institutionalized.

Tasks and Measures

Balloon Emotional Learning Task (BELT; Humphreys et al., 2013). Participants completed a computerized risky decision-making task with three different color balloon conditions (counterbalanced across participants), each with a different corresponding explosion point (7 = restricted; either 7, 13, or 19 = variable, 19 = generous) to allow for the examination of differential strategy (exploration vs. exploitation) on task outcome. There were a total of nine trials per condition, and for each third of the task, there was an equal number of trials per condition. Participants were asked to press a button to "pump up" balloons and earn points based on the number of pumps for each of the 27 balloon trials (i.e., more pumps earned more points). After the first pump participants could press a button to "cash in" their pumps for points. Points accumulated from trial to trial. If participants pumped beyond a balloon's limit, an explosion occurred, resulting in the loss of all points for that trial. Participants were not told that colors signified different response contingencies, but were explicitly told that not all balloons pop at the same point. Exploration was assessed by the number of pumps made, as each pump consists of a risk for an unknown outcome. Exploitation was assessed by the number of cash ins, as that action is selecting a choice with a known outcome: that points accumulated will be saved. Though often conceptualized as opposing choices, it is possible in this task to have high levels of exploration and exploitation if one learns the appropriate stop points for each condition. The BELT demonstrated good concurrent validity in young adults, with moderate positive correlations between sensation seeking and BELT outcomes of interest (Humphreys et al., 2013), and was used to examine exploration and exploitation strategy choice in this study.

Screen for Child Anxiety Related Emotional Disorders (SCARED; Birmaher et al., 1997). Parents completed the 41-item rating scale in order to assess child anxiety symptoms. Items are rated on a three-point scale, with higher scores signifying more anxiety. This measure has been shown to have good internal consistency ($\alpha = .74$–.93) (Birmaher et al., 1997). For the purpose of the present study we examined the separation anxiety disorder total score.

Data Analysis

Separate repeated measures (three task conditions) ANOVA models were examined for three variables: (1) pumps (proportion pumps out of total possible pumps), a measure of exploration, as greater pumps is a form of sampling the task environment, (2) percentage of trials that were cashed in, as a measure of exploitation, as cashing in any given trial is selecting a known and safe outcome, and (3) points (proportion earned points out of total possible points) as a measure of earnings. Where specified, group (PI vs. comparison), age, and sex were included in the models as fixed effects. Effect sizes are presented for all analyses, adjusted for age and sex when included in the model. In order to test whether separation anxiety mediated the association between PI status and exploitation, per expert recommendations (e.g., Hayes, 2009; MacKinnon, Fairchild, & Fritz, 2007) we conducted a single step test of mediation using SPSS PROCESS (Hayes, 2012). PI status (PI = 1, comparison = 0) was entered as the independent variable, exploitation was entered as the dependent variable, and separation anxiety was entered as the mediator. Both sex and age were included as

covariates. To assess the indirect effect, which is the amount separation anxiety mediated the association between PI status and degree of exploitation, a non-parametric bootstrap procedure using sampling with replacement ($n = 1,000$) was implemented and 95% bias corrected and accelerated confidence intervals (CI) were calculated for the indirect effect. If the CI does not include zero, the indirect effect is considered statistically significant.

RESULTS

Exploration, Exploitation, and Earnings

Task exploration, exploitation, and earnings were examined using repeated measures ANCOVAs with task condition (restricted, variable, and generous) as a repeated measure and PI status (PI vs. comparison youth) as a between subjects variable, covarying for age and sex. For overall exploration, the between subjects effect for PI status was significant, where PI youth pumped less than comparison youth ($F(1,133) = 11.12$, $p < .001$, $d = 0.58$, 95%CI [0.38, 1.11]) (Fig. 1). In addition, there was a significant between subjects effects of age ($F(1,133) = 8.77$, $p = .004$), such

that older children pumped more on the task. There was no between subjects effect of sex ($F(1,133) = 1.21$, $p = .27$). In addition, a marginal PI status by condition interaction was found ($F(2,266) = 2.89$, $p = .057$, thus analyses were reconducted within each condition separately (Fig. 2A). PI youth made significantly fewer pumps than comparison youths on all three conditions, though the magnitude of the difference was greatest on the restricted condition ($F(1,133) = 14.45$, $p < .001$, $d = 0.68$, 95%CI [0.29, 1.02]) followed by the variable condition ($F(1,133) = 9.11$, $p = .003$, $d = 0.55$, 95%CI [0.17, 0.89]), and then the generous condition ($F(1,133) = 4.35$, $p = .039$, $d = 0.38$, 95%CI [−0.06, 0.66]).

For exploitation (i.e., percentage of trials cashed in), there was a significant between subjects effect for PI status, as PI youth were more likely to "cash in" than comparison youth ($F(1,133) = 6.37$, $p = .013$, $d = −0.45$, 95%CI [−0.86, −0.14]) (Fig. 1). Age was unrelated to exploitation ($F(1,133) = 1.81$, $p = .18$). However, there was a significant between subjects effect of sex ($F(1,133) = 4.87$, $p = .029$), in which girls were significantly more likely to "cash in" than boys (.86 [.01] vs. .81 [.02]). In addition, a significant PI status by condition interaction was found ($F(2,266) = 4.03$, $p = .019$), thus analyses were reconducted within each
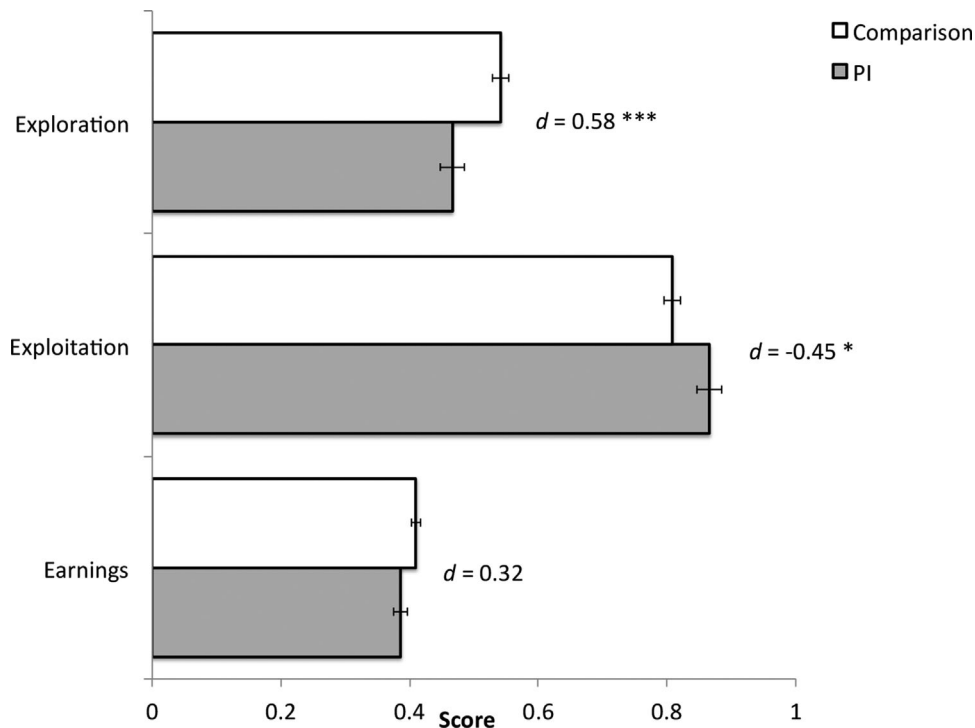

FIGURE 1 Overall exploration, exploitation, and earnings by group. Notes. Error bars denote ± 1 standard error of the mean. PI = previously-institutionalized. Score represents pumps out of possible pumps for exploration, percent of trials in which participants cashed in for exploitation, and points earned out of possible points for earnings. $^{*}p < .05$; $^{***}p < .001$.
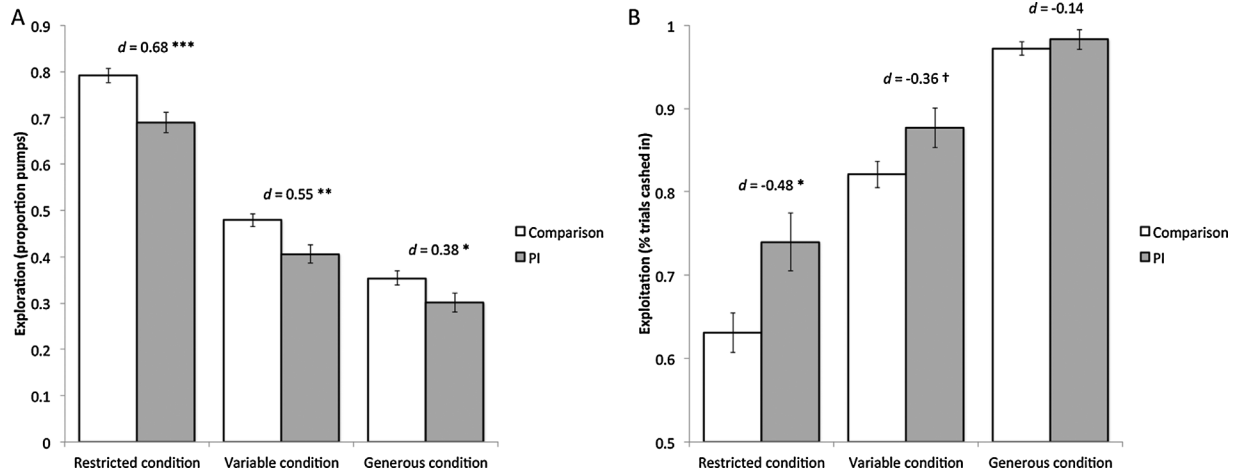
FIGURE 2 Exploration (A) and exploitation (B) by group and task condition. Notes. Error bars denote ± 1 standard error of the mean. PI = previously-institutionalized. $^{\dagger}p < .10$; $^{*}p < .05$; $^{**}p < .01$; $^{***}p < .001$.

condition separately (see Fig. 2B). A significant effect of PI status was found for the restricted condition ($F(1,133) = 6.67$, $p = .011$, $d = -0.48$, 95%CI [-0.97, -0.25]) and a marginal effect was found for the variable condition ($F(1,133) = 3.88$, $p = .051$, $d = -0.36$, 95%CI [-0.86, -0.14]). However, for the generous condition there was no group effect ($F(1,133) = .53$, $p = .47$, $d = -0.14$, 95%CI [-0.46, 0.25]).

For earnings (i.e., percentage of points earned out of possible points), age was significantly associated with earnings ($F(1,133) = 12.87$, $p < .001$), such that older ages earned more points on the task. There was a trend for the between subjects effects of sex ($F(1,133) = 3.72$, $p = .056$), in which girls earned marginally more points than boys (.41 [.01] vs. .39 [.01]). There was not a significant overall effect of PI status (Fig. 1) or a PI by condition interaction ($F(2,266) = 1.46$, $p = .24$).

Effect of Exploitation on Earnings

The two groups used different strategies across the task, but had roughly comparable earnings overall. Therefore, we examined whether certain strategies (i.e., increased exploitation) produced different outcomes on earnings as a function of task condition, regardless of group, sex, or age. As can be seen in Figure 3A–C, exploitation was differentially related to earnings based on task condition. For the restricted condition, greater exploitation was positively associated with earnings ($F(1,135) = 113.44$, $\beta = .68$, $p < .001$, $R^2 = .45$, 95%CI [.34, .58]). There was a small, but significant negative association between exploitation and earnings on the variable condition ($F(1,135) = 5.92$, $\beta = -.21$, $p = .02$,

$R^2 = .04$, 95% CI [.02, .10]). For the generous condition, exploitation was significantly associated with decreased earnings ($F(1,135) = 100.05$, $\beta = -.65$, $p < .001$, $R^2 = .43$, 95%CI [.31, .55]). Taken together, these analyses indicate that exploitation is adaptive for acquiring earnings under the restricted condition, but maladaptive under the other two conditions.

Separation Anxiety Mediates Early Adversity and Exploitation

We examined separation anxiety by group, controlling for sex and age, in participants with available data ($n = 125$). Controlling for sex and age, PI youth had significantly higher levels of separation anxiety than comparison youth ($F(1,121) = 8.42$, $p = .004$, $d = -0.54$, 95%CI [-0.91, -0.16]). There was a significant association between age and separation anxiety ($F(1,121) = 6.43$, $p = .012$), such that increasing age predicted lower levels of anxiety. Sex was not related to separation anxiety ($F(1,121) = 2.70$, $p = .10$). Separation anxiety was examined as a mediator of the association between dummy-coded PI status on exploitation. In our mediation analysis, the full model was significant, $F(4,120) = 4.49$, $p = .002$, accounting for 36% of variance in exploitation. Figure 4 provides a summary of the unstandardized regression coefficients and standard errors for each path. The 95%CI for the indirect effect of separation anxiety was small, but did not contain zero (point estimate = .01 [.01], 95%CI [.003, .03], thus, it can be concluded that the separation anxiety mediated the association between PI status and exploitation.
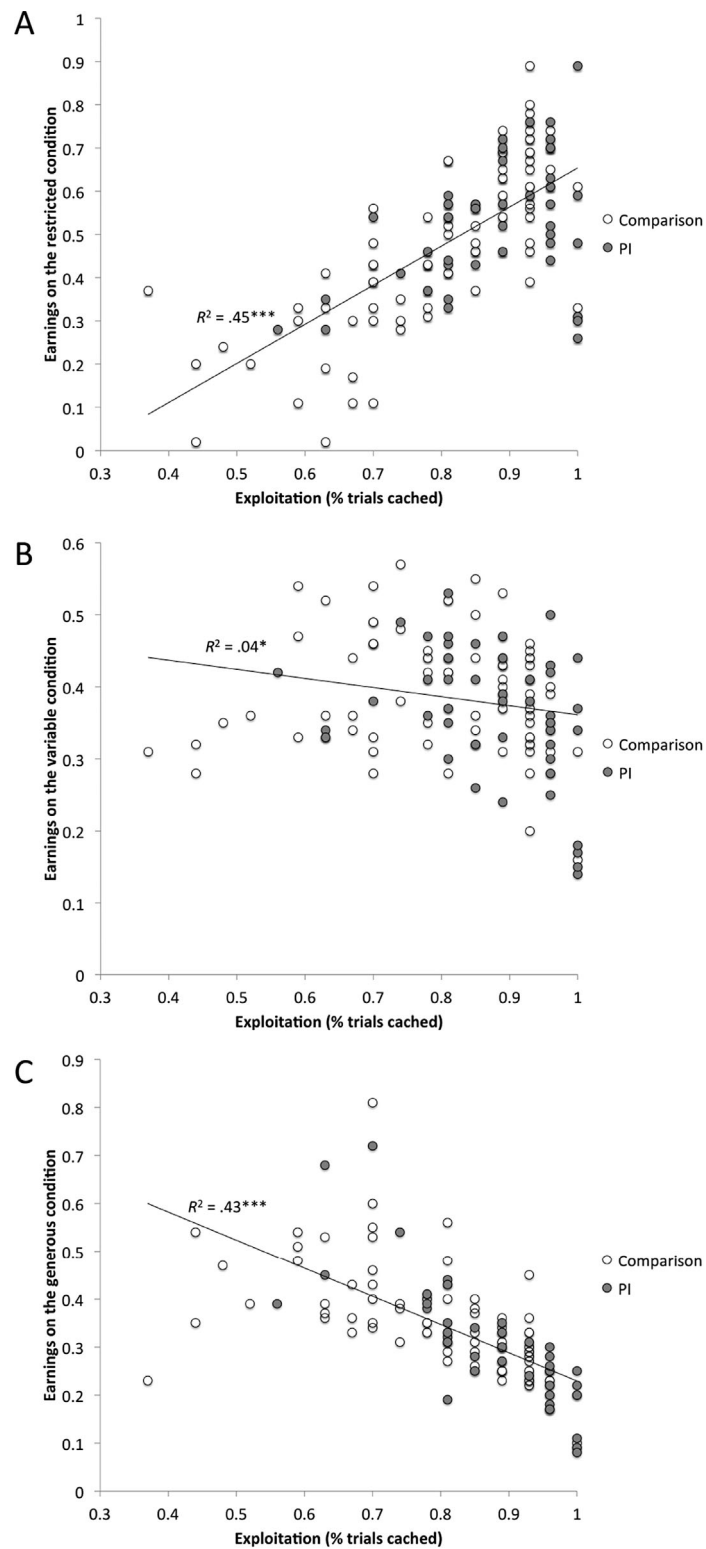
FIGURE 3 The association between overall exploitation and earnings on the restricted condition (A), variable condition (B), and generous condition (C). Notes. PI = previously-institutionalized. $^{*}p < .05$; $^{***}p < .001$.
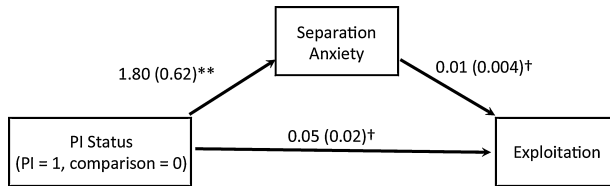
FIGURE 4 Mediation model for group status, separation anxiety, and exploitation. Notes. Unstandardized regression coefficients (SE). PI = previously-institutionalized. $^{\dagger}p < .10$; $^{**}p < .01$.

Supplemental Analyses

Analyses were repeated in the sample of youths without medication given group differences in medication rates. The findings were essentially unchanged, with the exception that the separation anxiety mediation of PI status and exploitation was somewhat reduced, as the indirect effect now included zero (95%CI [−.001, .02]), likely because medicated PI youth have higher anxiety than those PIs without medications ($F(1,39) = 5.89$, $p = .023$, $d = 1.01$, 95%CI [0.23, 1.75]). PI youth with and without current psychotropic medication were comparable in exploration, exploitation, and earnings (ps > .10). In addition, length of institutionalization was found to be unrelated to all task outcomes and social anxiety, and the removal of individuals with a length of institutionalization beyond two standard deviations from the mean resulted in unchanged findings.

DISCUSSION

These findings suggest that previous institutionalization was associated with differential exploration—exploitation strategy, with PI youth having exhibited significantly less explorative and more exploitative behavior than comparison youth who never experienced institutional care. Strategy choice resulted in differential success, depending on context; under a restricted condition, increased exploitation resulted in higher earnings, whereas under a generous condition exploitation predicted lower earnings. The bias towards exploitation (selection of the limited but reward-promising outcome) found in PI youth was mediated by heightened separation anxiety, one of the most common phenotypes following early institutional caregiving. This study indicates that heightened anxiety may be a developmental adaptation following early adversity guiding a bias toward exploitation, which is a useful behavioral strategy in certain contexts.

Institutional care limits the establishment of a secure attachment base (Hostinar & Gunnar, 2013; Zeanah, Berlin, & Boris, 2011), which would normally encour-

age exploration (Bowlby, 2008). The heightened anxiety associated with this early caregiving was found to be associated with the resultant exploration—exploitation strategy employed by the PI youth. Recent work has documented that the impact of this atypical early experience has long-term effects on neural development associated with anxiety (e.g., amygdala and medial prefrontal cortex; Gee et al., 2013; Tottenham et al., 2010, 2011). Although developmental psychopathology models typically emphasize phenotypes following early adversity as negative consequences of early environment (e.g., heightened anxiety), these phenotypes may be ontogenetic adaptations to the environment. As such, separation anxiety may be a developmentally appropriate reaction to early caregiving disruptions (Bowlby, 1961).

Though there is some evidence of increased risk-taking, a form of exploration, following early adversity (e.g., Sujan, Humphreys, Ray, & Lee, 2014), frameworks for understanding differences in goal-directed behavior in varied contexts may help to understand the more risk averse behavior observed in PI samples. Work on the regulatory focus theory (Higgins, 1997, 1998) proposes that goal-directed behavior is regulated by two difference systems: promotion and prevention, orienting to goals of gains and losses, respectively. In this model of decision-making, we expect that individuals with a prevention focus (e.g., those with elevated anxiety) to behave conservatively in order to reduce losses and assure safety (Crowe & Higgins, 1997). The behavior observed in the PI youth may be more in line with prevention-focused behavior as their behavior emphasizes the immediate earnings via heightened exploitation at the cost of potentially even higher earnings. Specifically, atypical phenotypes may be adaptive for survival based on expectations of the future environment (Belsky, Steinberg, & Draper, 1991; Boyce & Ellis, 2005; Frankenhuis & Del Giudice, 2012; Ellis & Del Giudice, 2014), and neural circuits in those who experienced early adversity are postulated to prepare for difference challenges than those without early adverse experiences (Ganguly & Brenhouse, 2014).

We predicted that early experience in the form of prior institutional care would result in altered decision-making in the context of risk. The hypothesis, based on work indicating that ontogenetic adaptations occur in response to maternal separation in early life (Callaghan & Richardson, 2011), highlights that future behavior is shaped by early experience. Clearly, the best strategy for balancing exploration and exploitation is highly dependent on one's environment. Traditional decision-making science indicates that, under stable economic conditions, one should value a larger long-term outcome over a smaller immediate payout (Cohen,

McClure, & Yu, 2007). Yet, under conditions of uncertainty, the more adaptive choice may be to retrieve immediate reward rather than risk a loss after delay. Whether risk-taking is adaptive or maladaptive depends on context, and thus risk-taking strategies are likely to be influenced by environmental cues (Ellis et al., 2012). Empirical studies have been examined to test biological sensitivity to context, and data from two longitudinal studies show general support that children differentially calibrate responses to the environment in a manner consistent with expectations from early experiences (see Ellis, Essex, & Boyce, 2005). The present study used a laboratory-based computerized task to experimentally manipulate contexts in which exploration and exploitation may be differentially successful approaches, and provided additional support that early experience predicts behavior in a way consistent with conditional adaptation. Early experiences characterized by deprivation may tune the developing brain to expect a future deprived environment, thereby resulting in increased exploitation. The inclusion of an adopted sample that did not experience institutionalization would be helpful in disentangling the effects of deprivation from differences related to a change in caregivers.

CONCLUSION

Traditional approaches to developmental psychopathology emphasize the negative phenotypic sequelae of early adversity. However, our results provide support that more conservative exploration—exploitation strategies may be conditionally adaptive (in line with expectations based on the early environment) following previous institutionalization, and that such strategy choice appears to result in context dependent success. As a result, decreased exploration in favor of exploitation may be viewed not simply as atypical, but rather as a developmental adaptation suited for a stressful and uncertain environment.

REFERENCES

Belsky, J., Steinberg, L., & Draper, P. (1991). Childhood experience, interpersonal development, and reproductive strategy: And evolutionary theory of socialization. Child Development, 62, 647–670. doi: 10.1111/1467–8624. ep9109162242.

Birmaher, B., Khetarpal, S., Brent, D., Cully, M., Balach, L., Kaufman, J., & Neer, S. M. (1997). The screen for child anxiety related emotional disorders (SCARED): Scale construction and psychometric characteristics. Journal of

the American Academy of Child and Adolescent Psychiatry, 36, 545–553. doi: 10.1097/00004583–199704000-00018.

Bowlby, J. (1961). Separation anxiety: A critical review of the literature. Journal of Child Psychology and Psychiatry, 1, 251–269. doi: 10.1111/j.1469–7610.1960.tb01999.x.

Bowlby, J. (2008). A secure base: Parent-child attachment and healthy human development. New York: Basic Books.

Boyce, W. T., & Ellis, B. J. (2005). Biological sensitivity to context: I An evolutionary – developmental theory of the origins and functions of stress reactivity. Development and Psychopathology, 17(2), 271–301. doi: 10.10170S0954579405050145

Callaghan, B. L., & Richardson, R. (2011). Maternal separation results in early emergence of adult-like fear and extinction learning in infant rats. Behavioral Neuroscience, 125, 20–28. doi: 10.1037/a0022008.

Cicchetti, D., & Rogosch, F. A. (2001). The impact of child maltreatment and psychopathology on neuroendocrine functioning. Development and Psychopathology, 13 (4), 783–804.

Cohen, J. D., McClure, S. M., & Yu, A. J. (2007). Should I stay or should I go? How the human brain manages the trade-off between exploitation and exploration. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 362, 933–942. doi: 10.1098/rstb.2007.2098.

Crowe, E., & Higgins, E. T. (1997). Regulatory focus and strategic inclinations: Promotion and prevention in decision-making. Organizational Behavior and Human Decision Processes, 69, 117–132. doi: 10.1006/obhd.1996.2675.

Elliott, A., & McMahon, C. (2011). Anxiety among an australian sample of young girls adopted from china. Adoption Quarterly, 14(3), 161–180. doi: 10.1080/10926755.2011.560792.

Ellis, B. J., & Del Giudice, M. (2014). Beyond allostatic load: Rethinking the role of stress in regulating human development. Development and Psychopathology, 26, 1–20. doi: 10.1017/S0954579413000849.

Ellis, B. J., Del Giudice, M., Dishion, T. J., Figueredo, A. J., Gray, P., Griskevicius, V., … & Wilson, D. S. (2012). The evolutionary basis of risky adolescent behavior: Implications for science, policy, and practice. Developmental Psychology, 48 (3), 598–623. doi: 10.1037/a0026220.

Ellis, B. J., Essex, M. J., & Boyce, W. T. (2005). Biological sensitivity to context: II. Empirical explorations of an evolutionary-developmental theory. Development and Psychopathology, 17 (2), 303–28. Retrieved from. http://www.ncbi.nlm.nih.gov/pubmed/16761547.

Frankenhuis, W. E., & Del Giudice, M. (2012). When do adaptive developmental mechanisms yield maladaptive outcomes. Developmental Psychology, 48 (3), 628–642. doi: 10.1037/a0025629.

Ganguly, P., & Brenhouse, H. C. (2014). Broken or maladaptive? Altered trajectories in neuroinflammation and behavior after early life adversity. Developmental Cognitive Neuroscience, 11, 18–30. doi: 10.1016/j.dcn.2014.07.001.

Gee, D. G., Gabard-Durnam, L. J., Flannery, J., Goff, B., Humphreys, K. L., Telzer, E. H., … & Tottenham, N.

(2013). Early developmental emergence of human amygdala-prefrontal connectivity after maternal deprivation. Proceedings of the National Academy of Sciences of the United States of America, 110 (39), 15638–15643. doi: 10.1073/pnas.1307893110.

Glass, B. D., Maddox, W. T., Bowen, C., Savarie, Z. R., Matthews, M. D., Markman, A. B., & Schnyer, D. M. (2011). The effects of 24-hour sleep deprivation on the exploration–exploitation trade-off. Biological Rhythm Research, 42, 99–110. doi: 10.1080/09291011003726532.

Goff, B., Gee, D. G., Telzer, E. H., Humphreys, K. L., Flannery, J., Tottenham, N., & Gabard-durnam, L. (2012). Reduced nucleus accumbens reactivity and adolescent depression following early-life stress United States of America.

Gunnar, M. R., Bruce, J., & Grotevant, H. D. (2000). International adoption of institutionally reared children: Research and policy. Development and Psychopathology, 12, 677–693. doi: 10.1017/S0954579400004077.

Hayes, A. F. (2012). PROCESS: A versatile computational tool for observed variable moderation, mediation, and conditional process modeling. Manuscript submitted for publication. (pp. 1–39). Retrieved from http://www.afhayes.com/public/process2012.pdf

Hayes, A. F. (2009). Beyond Baron and Kenny: Statistical mediation analysis in the new millennium. Communication Monographs, 76, 408–420. doi: 10.1080/03637750903310360.

Henning, E. R., Turk, C. L., Mennin, D. S., Fresco, D. M., & Heimberg, R. G. (2007). Impairment and quality of life in individuals with generalized anxiety disorder. Depression and Anxiety, 24, 342–349. doi: 10.1002/da.20249.

Higgins, E. T. (1997). Beyond pleasure and pain. The American Psychologist, 52, 1280–1300. doi: 10.1037/0003–066X.52.12.1280.

Higgins, E. T. (1998). Promotion and prevention: Regulatory focus as a motivational principle. Advances in Experimental Social Psychology, 30, 1–46. doi: 10.1016/S0065–2601 (08) 60381–0.

Hostinar, C. E., & Gunnar, M. R. (2013). The developmental effects of early life stress: An overview of current theoretical frameworks. Current Directions in Psychological Science, 22 (5), 400–406. doi: 10.1177/0963721413488889.

Humphreys, K. L., Lee, S. S., & Tottenham, N. (2013). Not all risk taking behavior is bad: Associative sensitivity predicts learning during risk taking among high sensation seekers. Personality and Individual Differences, 54, 709–715. doi: 10.1016/j.paid.2012.11.031.

Lejuez, C. W., Read, J. P., Kahler, C. W., Richards, J. B., Ramsey, S. E., Stuart, G. L., … & Brown, R. A. (2002). Evaluation of a behavioral measure of risk taking: The balloon analogue risk task (BART). Journal of Experimental Psychology, 8, 75–84. doi: 10.1037/1076–898X.8.2.75.

Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology. doi: 10.1139/z90–092.

Loman, M. M., Johnson, A. E., Quevedo, K., Lafavor, T. L., & Gunnar, M. R. (2014). Risk-taking and sensation-seeking propensity in postinstitutionalized early adolescents. Journal of Child Psychology and Psychiatry, 55, 1145–1152.

Luksys, G., Gerstner, W., & Sandi, C. (2009). Stress, genotype and norepinephrine in the prediction of mouse behavior using reinforcement learning. Nature Neuroscience, 12, 1180–1186. doi: 10.1038/nn.2374.

MacKinnon, D. P., Fairchild, A. J., & Fritz, M. S. (2007). Mediation analysis. Annual Review of Psychology, 58, 593–614. doi: 10.1146/annurev.psych.58.110405.085542.

Öhman A. (2000). Fear and anxiety: Evolutionary, cognitive, and clinical perspectives. In Handbook of Emotions (2nd ed.). New York: Guilford Press. pp. 573–593.

Raghunathan, R., & Pham, M. (1999). All negative moods are not equal: Motivational influences of anxiety and sadness on decision making. Organizational Behavior and Human Decision Processes, 79, 56–77. doi: 10.1006/obhd.1999.2838.

Shackman, J. E., Shackman, A. J., & Pollak, S. D. (2007). Physical abuse amplifies attention to threat and increases anxiety in children. Emotion, 7 (4), 838–852. doi: 10.1037/1528–3542.7.4.838.

Shonkoff, J. P., & Garner, A. S. (2012). The lifelong effects of early childhood adversity and toxic stress. Pediatrics, 129 (1), e232–e246. doi: 10.1542/peds.2011–2663.

Spivey, J., Barrett, D., Padilla, E., & Gonzalez-Lima, F. (2008). Mother-infant separation leads to hypoactive behavior in adolescent Holtzman rats. Behavioural Processes, 79, 59–65. doi: 10.1016/j.beproc.2008.05.002.

Sujan, A. C., Humphreys, K. L., Ray, L. A., & Lee, S. S. (2014). Differential association of child abuse with self-reported versus laboratory-based impulsivity and risk-taking in young adulthood. Child Maltreatment, 19, 145–155. doi: 1077559514543827.

Tottenham, N. (2013). The importance of early experiences for neuro-affective development. Current Topics in Behavioral Neurosciences. doi: 10.1007/7854_2013_254.

Tottenham, N., Hare, T. A., Millner, A., Gilhooly, T., Zevin, J. D., & Casey, B. J. (2011). Elevated amygdala response to faces following early deprivation. Developmental Science, 14, 190–204. doi: 10.1111/j.1467–7687.2010.00971.x.

Tottenham, N., Hare, T. A., Quinn, B. T., McCarry, T. W., Nurse, M., Gilhooly, T., … & Casey, B. J. (2010). Prolonged institutional rearing is associated with atypically large amygdala volume and difficulties in emotion regulation. Developmental Science, 13, 46–61. doi: 10.1111/j.1467–7687.2009.00852.x.

Census Bureau U. S. (2012). Statistical Abstract of the United States.

Wechsler D. (1999). The Wechsler Abbreviated Scale of Intelligence. New York: Psychological Corporation.

Zeanah, C. H., Berlin, L. J., & Boris, N. W. (2011). Practitioner review: Clinical applications of attachment theory and research for infants and young children. Journal of Child Psychology and Psychiatry, 52, 819–833. doi: 10.1111/j.1469–7610.2011.02399.x.

Zou, X., Scholer, A. A., & Higgins, E. T. (2014). In pursuit of progress: Promotion motivation and risk preference in the domain of gains. Journal of Personality and Social Psychology, 106, 183–201. doi: 10.1037/a0035391.