PAPER



Check for updates

Children's altruism following acute stress: The role of autonomic nervous system activity and social support

Nicholas V. Alen | LillyBelle K. Deer | Mona Karimi | Elis Feyzieva | Paul D. Hastings 💿 | Camelia E. Hostinar 💿

Psychology Department and Center for Mind and Brain, University of California, Davis, CA, USA

Correspondence

Nicholas V. Alen and Camelia E. Hostinar, Center for Mind and Brain, University of California, Davis, 202 Cousteau Place. Davis, CA 95618, USA. Email: nvalen@ucdavis.edu (N. V. A.) and cehostinar@ucdavis.edu (C. E. H.)

Abstract

Altruistic behavior after stress exposure may have important health and psychological benefits, in addition to broader societal consequences. However, so far experimental research on altruism following acute stress has been limited to adult populations. The current study utilized an experimental design to investigate how altruistic donation behavior among children may be influenced by (a) exposure to an acute social stressor, the Trier Social Stress Test modified for use with children (TSST-M), (b) individual differences in stress physiology, and (c) social support from a parent. The sample consisted of 180 children (54.9% male, 45.1% female; mean age = 9.92 years, SD = 0.56 years) randomly assigned to one of three conditions involving the TSST-M: (a) prepare for the TSST-M alone, (b) prepare for the TSST-M with a parent, and (c) no-stress control group. Results revealed that children made larger donations poststressor if they were alone before the acute stressor, if they had moderate cardiac autonomic balance, reflecting both parasympathetic and sympathetic influence, and if they were older. Children who prepared for the TSST-M with social support from a parent made comparable donations as children in the no-stress control group, in accord with stress buffering models. Increased altruism following acute stress among children suggests that a comprehensive understanding of the human stress response needs to incorporate "tend-and-befriend" behavior-the tendency for humans to show increased altruistic behavior during times of distress.

KEYWORDS

acute stress, altruism, autonomic nervous system, cardiac autonomic balance, prosocial behavior, social support

INTRODUCTION 1 |

Human altruism, defined as behavior that helps others at a cost to the self (Hastings et al., 2015), has widespread societal implications, particularly in times of crisis. For instance, some individuals responded to the COVID-19 pandemic with an increased urgency to donate their resources and time to help others and defeat the common threat, whereas others responded by stockpiling resources for themselves (Bavel et al., 2020; Tiffany, 2020). Thus, understanding the developmental origins of altruism and individual differences in altruistic behavior in the aftermath of acute stress may have important applications. Previous developmental research has shown that 9-year-old children, but not 6-year-old children, exhibit increased altruism following exposure to a natural disaster (Li et al., 2013). Furthermore, biopsychosocial perspectives have highlighted the role of social-contextual factors and individual differences in stress

physiology in the development of altruism (Miller & Hastings, 2016). However, so far altruistic behavior following acute stress has yet to be studied with experimentally controlled designs in children. In order to address this gap, the current study investigated children's altruism utilizing a biopsychosocial design by (a) measuring individual differences in stress physiology and (b) experimentally manipulating exposure to stress and access to parental support prior to the stressor.

1.1 | Altruism following acute stress in adulthood

Although the effects of acute stress on altruistic behavior have not been experimentally investigated in children, a number of studies have been conducted in adults. Historically, stress was theorized to trigger exclusively antisocial behaviors, leading Cannon to label the stress response the "fight-or-flight" response (Cannon, 1932). Seven decades later, Taylor and colleagues proposed that humans can also respond to stress with "tend-and-befriend" behaviors, including increases in altruism and social affiliation (Taylor et al., 2000). Originally proposed as a behavioral response specific to females, "tend-and-befriend" tendencies have been subsequently documented in males after stress (von Dawans et al., 2012; Singer et al., 2017; Taylor, 2006).

The evidence for tend-and-befriend behavior following stress exposure in adults so far has been mixed, including evidence of either increased or decreased altruism in the aftermath of stress. For example, following exposure to an acute social stressor, adult males have been found to exhibit increased sharing behavior (von Dawans et al., 2012; Tomova et al., 2017), and to be more likely to donate to charity (Sollberger et al., 2016). Increased sharing has also been found in adult females exposed to acute stress (von Dawans et al., 2019). In contrast to these findings, decreased sharing and reciprocity have also been observed following acute stress exposure among adult males (Steinbeis et al., 2015; Vinkers et al., 2013). The limited, and somewhat mixed, evidence so far suggests the existence of individual differences that may explain this heterogeneity. This possibility is supported by evidence from the developmental literature linking altruism to individual variation in stress physiology, particularly autonomic nervous system (ANS) functioning.

1.2 | Stress physiology and altruism

Prosocial behaviors, and altruism specifically, have been linked to both baseline and reactivity levels of ANS functioning. Baseline (i.e., resting) levels of ANS physiology measure trait-like characteristics that reflect an individual's propensity to respond to and engage with environmental challenge or threat (Laborde et al., 2017). By contrast, ANS reactivity reflects a state-like characteristic of how an individual responds to a specific environmental challenge or task. Because reactivity measures are context-dependent, they need to be interpreted with consideration of the specific contextual demands

Research Highlights

- Children exposed to an acute social stressor exhibited increased altruistic donation behavior compared with controls.
- The availability of parental support prior to the acute stressor led to altruistic donation behavior similar to controls.
- Moderate baseline cardiac autonomic balance (CAB) predicted increased altruistic donation behavior compared with low or high levels of CAB.

(Laborde et al., 2017). For example, during threat exposure physiological responding should be expected, and therefore greater reactivity may reflect an adaptive response (Porges, 2007). By contrast, during mild social interactions high levels of physiological reactivity may reflect an overreaction, and therefore suggest a maladaptive response (Beauchaine et al., 2007; Hastings et al., 2008).

Physiological profiles characterized by more moderate baseline levels, or more flexible reactivity during social engagement, have been associated with greater prosociality and altruistic behavior (Miller, 2018). For example, 4-year-old children with more moderate baseline parasympathetic nervous system (PNS) activity have been found to engage in greater altruistic donation behavior, compared with either low or high baseline PNS activity (Miller et al., 2017). One explanation for this finding is that engaging in altruistic behavior reguires flexibly attending to others' distress, and then calmly shifting the attention away from one's own needs toward someone else's. Because of this, baseline PNS activity that is too high might prevent recognizing and attending to someone else's distress, whereas baseline PNS activity that is too low might result in an overreaction to the distress in others, impeding other-focused altruistic responding (Miller et al., 2017). Moderate baseline PNS activity has also been associated with greater parent-reported prosociality in 7-year-old children (Zhang & Wang, 2019) and preschoolers (Clark et al., 2016), and greater self-reported prosociality in children aged 4-7 years (Miller et al., 2017).

Evidence from studies of autonomic reactivity supports the previously discussed explanation for why moderate baseline parasympathetic activity predicts greater altruism or general prosociality. For example, patterns of greater parasympathetic withdrawal while deciding how much to donate to charity and greater parasympathetic augmentation (i.e., recovery) while making the subsequent donation have been associated with greater donation amount among preschoolers (Miller et al., 2015). This again suggests that costly helping requires initial physiological responding to the social challenge, followed by a return to calm during engagement with the social challenge. In addition, more flexible parasympathetic reactivity during an emotional film clip has been associated with greater observed sympathetic concern and prosocial behavior during a simulated accident paradigm (Miller et al., 2016), further suggesting that flexible physiological engagement is an important component underlying individual differences in prosocial and altruistic behaviors.

Less is known about the relation between sympathetic nervous system (SNS) activity and children's costly helping (i.e., altruism). However, SNS activity has been previously linked to general social and emotional functioning in youth and adults, albeit in inconsistent patterns. For example, higher baseline sympathetic activity has been associated with more externalizing problems in middle to late childhood (Bubier et al., 2009). By contrast, higher baseline sympathetic activity has also been linked to greater behavioral warmth in early adolescence (Diamond & Cribbet, 2013). Sympathetic reactivity studies have also revealed mixed results. For example, greater SNS reactivity has been associated with less self-reported sympathy and teacher-reported prosociality among kindergarteners (Eisenberg et al., 1996; Holmgren et al., 1998), and less peer-reported prosociality among 6-year-olds (Kalvin et al., 2016). By contrast, greater SNS reactivity has been linked to less anti-social behavior (bullying), and greater observed prosociality among pre-adolescents and adolescents (Diamond & Cribbet, 2013; Lambe et al., 2019), as well as greater altruism in adults (Hein et al., 2011). These conflicting results may be due to heterogeneity of methodology. Alternatively, they may reflect a similarly guadratic relation between SNS activity and prosocial behavior; whereby some amount of sympathetic recruitment is necessary for attending to social interactions, but too much SNS recruitment may interfere with an individual's ability to engage in calm, other-oriented, prosocial behavior.

A large portion of the developmental psychophysiology research presented so far has focused on investigating either the SNS or the PNS. However, there is added value in studying both branches of the ANS (i.e., parasympathetic and sympathetic) simultaneously (Quigley & Moore, 2018). Studying a single branch of the ANS in isolation cannot inform us of the other branch, as the PNS and SNS do not always work in perfect opposition (Berntson et al., 1991). In addition, if both parasympathetic and sympathetic activities are involved in flexibly mobilizing internal resources to facilitate altruistic responding, then testing how these systems function in combination is an important next step in researching the physiological correlates of altruism (Hastings et al., 2014, 2015). One promising method for capturing the activity of both ANS branches is the use of autonomic space indices, such as cardiac autonomic balance (CAB; Berntson et al., 1991, 2008). CAB can be calculated from simultaneous recordings of PNS and SNS modulation of the heart, providing a measure of the relative contribution of each ANS branch to autonomic regulation of cardiac activity (Berntson et al., 2008). In youth samples, differential CAB has been linked to psychopathology, such as post-traumatic stress (Cohen et al., 2020) and depression (Bylsma et al., 2015). However, we are not aware of any past research into the relation between CAB and altruism in children.

The hypothalamic-pituitary-adrenocortical (HPA) axis has also been previously implicated in prosocial behavior. Specifically, higher baseline salivary cortisol, an index of HPA activity, has been associated with more empathic responding among 6-year-olds (Apter-Levi et al., 2016). Additionally, several adult studies have looked at the Developmental Science

relation between HPA activity in response to an acute stressor, and subsequent altruism following the stressor, though results so far are mixed. One study found a positive relation between HPA reactivity to acute stress and altruism following the stressor (Sollberger et al., 2016), though most studies have found no relation (Brown et al., 2009; von Dawans et al., 2012; Simons et al., 2017). To clarify these inconsistent findings, it is important to test alternative models of the relation between HPA reactivity to acute stress and altruism. For example, quadratic models can test if moderate HPA responding predicts greater altruism. In addition, it would be important to extend the limited research base to include children. Finally, the "tend-andbefriend" hypothesis (Taylor, 2006) proposed that variation in ANS and HPA physiology may help explain altruistic behavior post-stress. Thus, a more nuanced investigation into the relation between stress physiology before and during an acute stressor, and the subsequent altruistic behavior may help determine if differential activation of these stress systems explains acute stress effects on altruism (i.e., tend-and-befriend tendencies), or if baseline levels of activity represent an individual difference measure that predicts altruism.

1.3 | Social support and altruism

In child and adolescent correlational studies, perceived availability of social support has been positively correlated with several measures of altruism, such as self-reported altruistic tendencies (de Guzman et al., 2012), and observed sharing behavior (Ensor & Hughes, 2010), as well as general prosocial behavior (Cauce et al., 1994; Ochi & Fujiwara, 2016; Stewart & Sun, 2004). Yet, the immediate availability of social support may not be related to behavior in the same way as the general sense that one has supportive relationships. We are aware of only one experimental study that has looked at social support and prosocial behavior. In this study, the use of social support-priming photos was not significantly associated with prosocial behavior among preschoolers (Brett, 2017), but it is possible that a social support-priming paradigm is not salient enough to affect subsequent behavior. Experimental manipulation of social support during stress tasks has been shown to affect physiological stress reactivity in children, such that children randomly assigned to receive parental support prior to an acute stressor exhibit reduced stress reactivity (Hostinar et al., 2014), a concept commonly referred to as social buffering (Hennessy et al., 2009). Currently we are not aware of any study that has examined how social support might influence the effect of acute stress on altruistic behavior, but given the "tend-and-befriend" hypothesis, provision of social support in stressful situations may be expected to influence altruistic behavior.

1.4 | Hypotheses

In line with previous evidence for a "tend-and-befriend" post-stress response, we hypothesized that children would exhibit increased altruistic behavior following an acute social stressor, compared with a control condition. We also hypothesized that altruistic behavior would be predicted by individual differences in autonomic functioning. Specifically, in line with previous evidence that a more moderate physiological profile predicts greater altruism, we expected to find a guadratic relation between baseline CAB and donation behavior, such that moderate baseline CAB, representing relative balance between the ANS branches, would predict increased altruism across conditions. In addition, we hypothesized that stress reactivity during the acute stressor would predict altruistic behavior following the stressor, such that greater altruism would be predicted by (a) more moderate levels of CAB during the acute stressor and the altruism task, while controlling for baseline levels of CAB, and (b) more moderate cortisol reactivity during the acute stressor. Lastly, we hypothesized that availability of social support would influence the effect of acute stress on altruism, though it should be noted that this aspect of the study was largely exploratory. Given previous findings of positive associations between social support and prosocial behavior (Ensor & Hughes, 2010), we considered it possible that receiving social support in the laboratory would lead to increased altruistic behavior. Alternatively, considering social buffering, where availability of social support leads to decreased stress reactivity (Hostinar et al., 2014), and the positive association between cortisol and altruism found in one study (Sollberger et al., 2016), we also considered it possible that availability of social support would lead to less altruism following threat.

2 | METHODS

2.1 | Participants

This study included 181 children recruited from the Sacramento-Davis area through the University of California, Davis Participant Pool system, and advertisements on Facebook. One participant withdrew from the study shortly after arrival at the laboratory, before providing any data involved in the current analysis. The final sample consisted of 180 children (50.6% male, 49.4% female based on sex assigned at birth; 50% identified as boys, 48.9% as girls, and 1.1% as non-binary; Mean age = 9.91 years, *SD* = 0.57), each with an accompanying parent (165 mothers and 15 fathers). Phone interviews were conducted to screen for exclusion criteria, which included developmental disorder, chronic health condition, speech or



language disorder, and currently taking psychotropic or steroid medication. This analysis was part of a larger study examining the social and emotional development of children. The study was approved by the Institutional Review Boards of the University of California-Davis and the State of California Committee for the Protection of Human Subjects. Upon completion of the study, participants were given \$90, and an opportunity to keep an additional \$10 used in the donation task.

2.2 | Procedure

Experiments were performed in late afternoon (time of arrival ranged from 1:00 p.m. to 2:30 p.m.). Upon arrival at the laboratory, informed consent was obtained from the participant's parent or guardian, and informed assent was obtained from the participant. An hour after arrival, participants were attached to an ambulatory electrocardiograph (ECG) for the collection of autonomic physiology data, described in a following section. Participants were randomly assigned to one of three stress conditions involving the Trier Social Stress Test-Modified for children (TSST-M), an acute social stressor (please see description in the next section): (a) in the alone condition (n = 60), participants prepared for the TSST-M speech in a room alone, (b) in the *parent* condition (n = 59), participants prepared for the TSST-M speech in a room with a parent or guardian (53 mothers and 6 fathers), who was instructed to provide any assistance or support that felt natural to them, and (c) in the *control* condition (n = 61), participants engaged in a stress-free placebo version of the TSST-M. Fifteen minutes following the TSST-M or placebo, participants engaged in an altruistic donation task, as described below. For a timeline of the study visit, please see Figure 1.

2.3 | Trier social stress test-modified (TSST-M)

The TSST-M is a modified version of the Trier Social Stress Test (TSST) acute social stressor for adults (Kirschbaum et al., 1993), which was specifically designed to elicit a mild stress response in children in this age range (Yim et al., 2010). The TSST-M procedure utilized in the current study has been previously described in detail (Alen et al., 2020). Briefly, the procedure consisted of the following steps: participants were told that they had 10 min to prepare a

FIGURE 1 Timeline of study visit. Blue drops represent saliva collection timepoints. ECG, electrocardiogram; IMP, impedance; SAM, Self-Assessment Mannequin subjective stress measure; TSST-M, Trier Social Stress Test-Modified for children speech that would be evaluated by judges. After the 10-min preparation period, participants were taken to a novel room where there were two judges and a video camera. The participant then engaged in a 5-min speech followed by a 5-min arithmetic subtraction task. Judges refrained from showing facial affect or providing feedback to the child during the process.

Children randomly assigned to the *control* condition engaged in a placebo TSST-M that consisted of the following steps: participants were informed that they were part of a stress-free comparison group and were asked to spend 10 min thinking about their favorite book or movie. Following this 10-min period, participants were taken to a novel room where they engaged in 5 min of friendly conversation about the chosen book or movie with the experimenter. The participants were then asked to play a Sudoku game (level: easy) for 5 min; participants were told that their performance on the Sudoku was not important.

2.4 | Measures

Demographic information was obtained from parent questionnaires, which included child age, sex, and family income. Family income was indexed as yearly family income from jobs.

2.4.1 | Respiratory sinus arrhythmia

Respiratory sinus arrhythmia (RSA) is a measure of the beat-to-beat changes in heart rate, within the normal heart rate fluctuations associated with respiration (Berntson et al., 1997). RSA is often used to index parasympathetic nervous system (PNS) modulation, via the vagus nerve, of cardiovascular activity (Laborde et al., 2017). RSA was collected with a MindWare ambulatory electrocardiograph (ECG), using three silver electrodes with a 7% chloride wet gel attached to the child's chest. RSA data were collected as part of a larger physiology data collection procedure, including a 5-min baseline period, a 10-min TSST-M preparation period, a 10-min TSST-M task period, a cognitive task period, and an altruism task period; current analyses focused on the baseline, TSST-M or placebo task, and altruism periods. Baseline RSA data were collected in a seated position on a comfortable couch prior to administering the TSST-M instructions. Participants were instructed to not engage in any activity, to refrain from speaking to their parent, who was present, and to attempt to relax for the 5-min duration.

Interbeat Interval (IBI) data were calculated using an automated algorithm in the MindWare Biolab acquisition software. A highfrequency band pass filter set at 0.23–0.50 Hz was used to correspond to the breathing rate of this age range (Shader et al., 2018). Sampling rate was set at 250 Hz. R-peaks were inspected and cleaned for artifacts by trained researchers using MindWare Heart Rate Variability software. Arrhythmias (i.e., ectopic beats, sinus pauses) were corrected using the MindWare mid-beat function, which averages the IBI interval and minimizes the influence of artifacts. RSA Developmental Science

was calculated, using a Fast Fourier transformation algorithm, in 60-s epochs (Bernston et al., 1997). A 60-s epoch was considered usable when it met two criteria: (a) at least 30-s of clean, continuous data were available, and (b) less than 10% of R-peaks were estimated (e.g., using the mid-beat function). Manual inspection of peak breathing rate within each 60-s epoch ensured that participant breathing rate did not fall outside of the high-frequency band pass filter range. RSA during the individual 60-s epochs was then averaged together within each task, producing mean RSA values for the (a) baseline, (b) TSST-M, and (c) altruism tasks. Twenty participants were missing RSA data for one or more tasks due to ECG technical malfunction (n = 7), participant request to remove ECG electrodes (n = 5), participant declining to participate in the task (n = 5), and less than 30-s of clean, continuous data available (n = 3); this resulted in RSA data being available for: baseline (n = 173), TSST-M (n = 166), and altruism task (n = 164).

2.4.2 | Pre-ejection period

Pre-ejection period (PEP) was utilized as a marker of sympathetic activity, where shorter PEP is reflective of greater SNS modulation of cardiac activity (Berntson et al., 2004). PEP was calculated from cardiac impedance data measured concurrently to ECG data collection using a MindWare ambulatory device (MindWare, Westerville, OH). Four silver electrodes with a 7% chloride wet gel were attached to the child's chest and back in standard configuration (Sherwood et al., 1990). The impedance signal was used to derive dZ/dt, the first derivative of the change in thoracic impedance. PEP was defined as the amount of time in milliseconds between the Q-wave of the ECG signal and the B-notch of the dZ/dt signal (Berntson et al., 2004). For the identification of the B-notch, we employed an estimation method recommended by Lozano et al. (2007). Specifically, the B-notch was estimated using a percentage of the R-peak to Z-peak interval (RZ interval) in milliseconds plus a constant set at 4 milliseconds: B-notch = 0.55*RZ interval +4, (Lozano et al., 2007). Current analysis focused on PEP data during (a) a seated baseline period, (b) the TSST-M, and (c) the altruism task. Thirty-nine participants were missing PEP data for one or more tasks for the following reasons: impedance cardiogram technical malfunction (n = 13), less than 30 s of clean data available (n = 16), participant request to remove impedance electrodes (n = 5), and participant declining to participate in task (n = 5). This resulted in PEP data being available for baseline (n = 159), TSST-M (n = 151), and altruism task (n = 148).

2.4.3 | Cardiac autonomic balance

Cardiac autonomic balance (CAB) is a widely used metric that reflects the relative contributions of each branch of the ANS (i.e., sympathetic and parasympathetic; Quigley & Moore, 2018). CAB values were calculated from simultaneous recordings of RSA and PEP using the method previously described by Berntson et al. (2008). RSA and PEP values within each task were first z-scored to account for their different scales. RSA is positively related to parasympathetic activity, whereas PEP is negatively related to sympathetic activity. We therefore multiplied z-scored PEP (zPEP) by -1, so that both indices would be positively related to activity of their respective ANS branch. CAB was then calculated as a difference score: CAB = zRSA-(-zPEP). CAB values were calculated for: baseline, TSST-M, and the altruism task. To test both linear and quadratic associations between CAB and altruism, we (a) mean-centered CAB values, which served as a linear term, and then (b) calculated the square of the mean-centered values to yield a quadratic term.

2.4.4 | Salivary cortisol

Saliva samples were collected via passive drool and stored at -80° C until being shipped for assaying. Saliva was collected every 20 min for a total of 8 samples (minutes after arrival at laboratory: 10, 30, 50, 70, 90, 110, 130, and 150). Samples were assayed at the Salimetrics' SalivaLab (Carlsbad, CA) using the Salimetrics Salivary Cortisol Assay Kit (Cat. No. 1–3002), without modifications to the manufacturer's protocol. Samples were assayed in duplicate and averaged. Intra-assay coefficient of variation (CV) was excellent (4.6%), as was the inter-assay CV (6%). Cortisol data were missing for one participant due to researcher error, resulting in complete cortisol data available for N = 179 participants.

The current analysis utilized cortisol reactivity, which was indexed through change in cortisol from sample 4 (taken directly before administration of the TSST-M or control condition) to sample 6 (taken 20 min following the TSST-M or control condition). Sample 4 included 3 outliers (above 4 *SD* from the mean); sample 6 included 2 outliers. Outliers were Winsorized to the highest value within 4 *SD* from the mean. Winsorized cortisol values were log-transformed to correct for positive skew. Cortisol reactivity was then calculated by subtracting sample 4 from sample 6, such that higher values represent greater increases in salivary cortisol from pre-TSST-M to 20 min post-TSST-M.

2.5 | Altruistic donation behavior

Altruistic donation behavior was measured using a modified version of a donation task previously used in studies on childhood altruism (Miller et al., 2015, 2017). The current paradigm is almost identical to the original, with the exception of the prize: we provided participants with cash instead of prize tokens to make this more developmentally tailored for 9- to 10-year-olds. Approximately 15 min following the end of the TSST-M or placebo, the donation task was administered. During the donation task participants were informed that in addition to the monetary compensation they were told earlier that they would receive for the day (\$90), because they had done such a great job on the day's tasks they had been awarded an extra

\$10, presented to them as 10 one-dollar bills in an envelope with their name on it. The following prompt was then given: "Wow, that's pretty amazing. But you know what? I have another job too. Sometimes I'm here working with kids like you, but sometimes I work in a hospital where there are a lot of children who are sick. I know they'd like to be able to come here and play our games, but they can't because they're sick and in the hospital. If you want to, you could share some of your dollars with the sick kids, so they can buy some games for themselves too. It's up to you. You could share all of your dollars, or some of them, or none of them. It's up to you." Participants were then presented with a donation box with a logo for St. Jude's Children's Hospital on it. To minimize social desirability bias, the camera was turned off and participants were left alone in the room to complete the task. After participants' departure at the end of the visit, the experimenter recorded the number of dollars donated in the box, which constitutes our dependent measure. One participant declined to participate in the altruism task; as such, donation data were available for N = 179 participants.

2.6 | Statistical analysis

Bivariate correlations and descriptive analyses were performed using Statistical Package for Social Sciences (SPSS) version 26. Regression analysis was performed using RStudio version 1.3.959, running the Lavaan package version 0.6. To test the effect of experimental condition on donation behavior, we conducted a multiple linear regression using two dummy coded variables representing the effect of the alone condition compared with controls, and the parent condition compared with controls. Donation values exhibited moderate positive skew (skewness = 0.85, SE = 0.18); values were therefore square root transformed. Transformed donation values were approximately symmetrical (skewness = -0.27, SE = 0.18; Bulmer, 1979). Square root transformed donation data were utilized in all analyses. However, study results were comparable using non-transformed data, and inferences were the same. The following demographic covariates were included in the model, due to previous research linking these variables to altruism: age, sex, and family income (Hastings, Miller, & Troxel, 2015; Miller et al., 2015). Family income was z-scored before entering it into the model.

To test the relation between individual differences in autonomic physiology and donation behavior, we conducted a stepwise linear regression. In step 1 we entered condition effect variables, covariates (age, sex, family income), and baseline CAB linear and quadratic terms in the model. In step 2, we added linear and quadratic terms for CAB values during the TSST-M task. Lastly, in step 3, linear and quadratic terms for CAB values during the donation task were included in the model. In line with standard practice, CAB values were mean-centered prior to calculating quadratic terms.

Lastly, we tested salivary cortisol reactivity as a predictor of donation behavior in a separate model. Donation values (square root transformed) were regressed on salivary cortisol reactivity. Quadratic terms for cortisol reactivity were included in the model. Cortisol reactivity values were mean-centered before calculating quadratic term. Dummy-coded condition effects, age, sex, and family income were included as covariates.

2.6.1 | Missing data handling

A Little's MCAR test was nonsignificant, chi-square = 75.27, df = 72, p = 0.37, consistent with a missing completely at random (MCAR) pattern. Due to missingness in CAB data, we employed Full Information Maximum Likelihood (FIML), which allowed us to utilize all available data. FIML is superior to multiple imputation in accounting for missing data (Enders & Bandalos, 2001). However, inferences were identical using either FIML or list-wise deletion for missing data handling.

2.6.2 | Exploratory analysis

Post hoc exploratory analysis was conducted to investigate relations between subjective stress and altruism, and between emotion regulation and altruism. For complete methods and descriptions of measures utilized in exploratory analysis, please see online supplemental material.

3 | RESULTS

Sample characteristics and demographics are presented in Table 1. The bivariate correlation matrix is presented in Table 2.

3.1 | TSST-M manipulation check

A previous report with non-overlapping analyses based on this sample (Parenteau et al., 2021) revealed a significant increase in cortisol for children in the alone condition and in the parent condition, and their cortisol reactivity was significantly greater compared with that of controls (see Figure S1). In addition to these prior analyses, we found evidence of expected autonomic reactivity to the TSST-M. Linear regression predicting CAB during the TSST-M, controlling for baseline CAB, revealed significant negative effects of being in the *alone* condition compared with controls, B = -0.83, SE = 0.19, p < 0.001, and in the *parent* condition compared with controls, B = -0.80, SE = 0.19, p < 0.001. A negative effect of the TSST-M on CAB reflects a shift in autonomic balance toward sympathetic dominance. Significant condition effects on subjective stress were also observed. Specifically, while controlling for baseline subjective stress levels, greater subjective stress was reported by children in the *alone* condition, compared with controls (B = 2.41, SE = 0.16, p < .001), and by children in the *parent* condition, compared with controls (B = 2.23, SE = 0.16, p < 0.001; see Figure S2). These results suggest that the TSST-M was successful in eliciting a stress response for both biological and subjective stress measures.

TABLE 1 Sample characteristics and study descriptives

Developmental Science 🛛 📸

	м	SD	Range
Donation Amount (\$)	3.50	2.92	0-10
Age in years	9.91	0.57	9.03-11.10
Family income (\$)	121,886	58,391	2,500- 200,000
Baseline RSA	6.62	1.15	3.83-9.33
Baseline PEP	79.74	10.04	42.67-106.80
Baseline CAB	0.02	1.44	-3.96-3.64
TSST-M RSA	5.71	1.17	2.91-9.15
TSST-M PEP	78.66	9.44	41.09-103.20
TSST-M CAB	0.02	1.54	-4.13-3.67
Altruism RSA	5.73	1.14	3.13-9.07
Altruism PEP	78.12	9.51	40.00-105.00
Altruism CAB	0.003	1.47	-4.18-3.51
Cortisol Reactivity	0.10	0.29	-0.46-1.06
	Level	Ν	%
Sex	Male	91	50.6
	Female	89	49.4
Race	Non-Hispanic White	115	64.2
	Mixed race/ ethnicity	43	24.0
	Asian	10	5.6
	Other race/ ethnicity	11	6.2

Abbreviations: CAB, cardiac autonomic balance; PEP, pre-ejection period; RSA, respiratory sinus arrhythmia; TSST-M, Trier Social Stress Test—modified for children.

3.2 | Effects of acute stress on altruism

Linear regression results (presented in Table 3) revealed a significant positive effect of being in the *alone* condition, compared with controls, on donation amount, B = 0.32, SE = 0.16, p = 0.047, 95% CI [0.004, 0.63]. Children in the alone condition donated more money than children in the control condition (see Figure 2). Children in the *parent* condition did not significantly differ in donation amount compared with controls, B = 0.11, SE = 0.16, p = 0.49. In addition, results revealed a significant positive relation between child age and donation behavior, with older children donating more than younger children across conditions, B = 0.41, SE = 0.11, p < 0.001, 95% CI [0.19, 0.64].

3.3 | Associations between stress physiology and altruism

Step-wise linear regression results, testing associations between CAB and donation amount, are presented in Table 4. In step 1, results revealed a nonsignificant linear estimate for baseline CAB in

	2	ო	4	5	6	7	œ	6	10	11	12	13	14	15	16	17
1. Donation	0.94**	0.31**	0.07	0.02	-0.02	0.06	0.001	-0.04	0.06	-0.02	-0.06	0.11	-0.03	0.05	0.08	14
2. (Sqrt) Donation	I	0.28**	0.10	0.00	-0.01	0.06	-0.01	-0.04	0.05	-0.03	-0.06	0.13	-0.02	0.06	0.10	00
3. Age		I	0.05	-0.03	0.09	-0.02	0.03	0.08	0.03	0.05	0.18	0.72	0.05	-0.18*	0.04	-0.07
4. Sex (female)			Ι	0.04	-0.14	0.002	-0.10	-0.12	-0.12	-0.17*	-0.11	-0.02	-0.10	0.14	0.08	-0.09
5. Family income				Ι	-0.03	-0.04	-0.05	-0.11	-0.03	-0.09	0.00	-0.05	-0.03	-0.08	0.02	-0.16*
6. Baseline RSA					I	0.06	0.72**	0.74**	0.15	0.58**	0.68**	0.11	0.51^{**}	-0.01	-0.06	0.02
7. Baseline PEP						I	0.74**	0.12	0.71**	0.54**	0.10	0.76**	0.57**	0.03	0.02	0.14
8. Baseline CAB							I	0.56**	0.59**	0.75**	0.50**	0.60**	0.73**	0.01	-0.01	0.11
9. TSST-M RSA								I	0.17*	0.77*	0.76*	0.10	0.58**	-0.21**	-0.31**	0.00
10. TSST-M PEP									I	0.76**	0.13	0.84**	0.67**	-0.04	-0.01	0.12
11. TSST-M CAB										I	0.57**	0.61**	0.81^{**}	-0.17*	-0.19*	0.07
12. Altruism RSA											I	0.10	0.74**	-0.24**	-0.11	0.01
13. Altruism PEP												Ι	0.75**	0.05	0.01	0.22**
14. Altruism CAB													I	-0.15	-0.06	0.15
15. Cortisol Reactiv	ity													I	0.37**	0.06
16. Subjective Stres	S														I	.06
17. Emotion Regulat	ion															I
bbreviations: CAB, o	ardiac autonomic	: balance; PI	EP, Pre-eje	ction peric	od; RSA, res	spiratory si	nus arrhyth	ımia; (Sqrt)	Donation,	square roo	t transform	ied donatio	n amount; ⁻	TSST-M, Tri	ier Social Str	ess Test-

modified for children. **p* < 0.05. ***p* < 0.01.

-WILEY- Developmental Science 57

TABLE 2 Bivariate correlation matrix

 TABLE 3
 Experimental condition effects on donation behavior

Predictor	В	SE	p-value	95% CI LL	95% CI UL
Alone TSST-M condition	0.32	0.16	0.047*	0.004	0.63
Parent TSST-M condition	0.11	0.16	0.49	-0.21	0.43
Age	0.41	0.11	< 0.001**	0.19	0.64
Sex (female)	0.15	0.13	0.26	-0.11	0.41
Family income	0.001	0.07	0.98	-0.13	0.13

Control condition served as reference group for estimating effects of Alone TSST-M and Parent TSST-M conditions.

Abbreviations: CI LL, lower limit of the 95% confidence interval; CI UL, upper limit of the 95% confidence interval.

*p < 0.05.

**p < 0.01.

predicting donation amount, B = -0.04, SE = 0.05, p = 0.48, and a significant and negative quadratic estimate, B = -0.08, SE = 0.02, p < 0.001, 95% CI [-0.12, -0.04], suggesting an inverse U-shaped curve (see Figure 3). The estimated peak of the inverse U-shaped curve was at the baseline CAB value of -0.21 (0.17 *SD* below the mean). A region of significance analysis, utilizing the Johnson Neyman technique (Miller et al., 2013), revealed that donation amount increased with increasing baseline CAB values up to -0.87 (0.63 *SD* below the mean), and, consistent with an inverted U pattern, decreased as baseline CAB values increased above 0.40 (0.26 *SD* above the mean).

In step 2, CAB from the TSST-M segment was included in the model and revealed a nonsignificant linear estimate, B = 0.04, SE = 0.07, p = 0.59, and a nonsignificant quadratic estimate, B = 0.002, SE = 0.03, p = 0.93. In step 3, CAB during the donation task was

Developmental Science

added to the model and also revealed a nonsignificant linear estimate, B = -.04, SE = 0.05, p = 0.48, and a nonsignificant quadratic estimate, B = -0.04, SE = 0.05, p = 0.48. In the final model, with all CAB values included, the baseline CAB quadratic estimate remained significant (p = 0.004).

Linear regression testing the relation between salivary cortisol reactivity and donation behavior found no significant linear or quadratic relation between cortisol reactivity and donation behavior. Specifically, results from this model revealed a nonsignificant linear estimate, B = 0.05, SE = 0.29, p = 0.86, and a nonsignificant quadratic estimate, B = 0.64, SE = 0.57, p = 0.26.

3.4 | Exploratory analysis

Results from our exploratory analysis predicting donation amount from subjective stress levels revealed a nonsignificant linear estimate, B = 0.01, p = 0.95, and a nonsignificant quadratic estimate, B = -0.03, p = 0.54. Exploratory analysis of the relation between emotion regulation and altruism revealed a nonsignificant association between emotion regulation and donation amount, B = 0.002, p = 0.87. In addition, the interaction terms were nonsignificant between the *alone* condition and emotion regulation, B = 0.01, p = 0.80, and between the *parent* condition and emotion regulation, B = -0.03, p = 0.50, suggesting emotion regulation did not moderate the effect of acute stress on donation amount.

4 | DISCUSSION

The current study aimed to investigate the influence of acute stress on altruistic donation behavior in late childhood, a period of





TABLE 4 Stepwise linear regression predicting donation amount from cardiac autonomic balance

	Step 1		Step 2			Step 3			
Predictor	В	SE	p-value	В	SE	p-value	В	SE	p-value
Alone TSST-M condition	0.36	0.15	0.02*	0.39	0.16	0.02*	0.40	0.16	0.01*
Parent TSST-M condition	0.05	0.15	0.76	0.08	0.16	0.63	0.10	0.17	0.57
Age	0.46	0.11	< 0.001**	0.45	0.11	< 0.001**	0.45	0.11	< 0.001**
Sex (female)	0.15	0.13	0.25	0.15	0.13	0.23	0.16	0.13	0.22
Family income	0.01	0.06	0.94	0.01	0.06	0.91	0.01	0.06	0.89
CAB baseline linear	-0.04	0.05	0.45	-0.07	0.08	0.37	-0.08	0.08	0.29
CAB baseline quadratic	-0.08	0.02	< 0.001**	-0.08	0.03	0.005**	-0.08	0.03	0.004**
CAB TSST-M linear				0.04	0.07	0.59	0.06	0.09	0.51
CAB TSST-M quadratic				0.002	0.03	0.93	0.01	0.03	0.83
CAB Altruism linear							-0.01	0.09	0.95
CAB Altruism quadratic							01	.04	.87

Abbreviations: CAB, cardiac autonomic balance; TSST-M, Trier Social Stress Test-modified for children.

*p < 0.05.

**p < 0.01.





increasing autonomy. While previous research has produced somewhat inconsistent results, a growing body of evidence suggests that following acute stress adults can exhibit increased altruistic behavior (von Dawans et al., 2012, 2019; Sollberger et al., 2016; Tomova et al., 2017), a behavioral response to stress previously described as "tend-and-befriend" (Taylor et al., 2000). Considering these past findings, we hypothesized that following an acute social stressor, children would similarly engage in increased altruistic behavior, measured through amount of dollars donated to charity.

Consistent with this hypothesis, we found that children exposed to the TSST-M tended to donate more of their "extra earnings" to charity compared with controls. We also discovered that this increase in altruism post-stress was specific to children who spent 10 min alone and did not receive social support from a parent while ALEN ET AL.

preparing for the TSST-M speech; children who were with their parent and received social support from a parent were not significantly different from children in the non-stress condition in their donation behavior. This additional finding is in line with previous evidence suggesting a positive association between stress reactivity and altruistic behavior (Sollberger et al., 2016), and reduced stress reactivity among children who receive support from their parents (Gunnar & Hostinar, 2015). It is possible that stress-related biological or cognitive mechanisms increasing the donation amount in the alone condition were inhibited by the availability of parental support in the parent condition. Consistent with this notion, previous studies have documented that social behavior following acute stress depends on the type or intensity of the stressor utilized (von Dawans et al., 2018; Potts et al., 2019). By drawing on the supportive presence of a primary caregiver and attachment figure, it is possible that the TSST-M in the parent condition was experienced by children as a milder stressor, and therefore failed to significantly affect donation behavior. It is also possible that children who received support from their parents may have retained their extra earnings to share with their parent.

Discovering that children in the *alone* condition donated the most provides evidence for "tend-and-befriend" behavior after acute stress and suggests that these prosocial behavioral responses to stress are present in childhood. Theories on why humans might engage in this behavior often point to the survival benefits associated with being a social species: in times of threat, humans band together for support to increase their individual survival odds (Taylor, 2006). Being alone for 10 min may also activate needs to become reintegrated within the social group, shifting social decision-making toward altruistic patterns. Theoretically, a social-affiliative stress response may be particularly important in childhood, when being kind to others in times of threat could result in increased protection and benevolence from others, increasing survival odds. Alternative

explanations for "tend-and-befriend" behavior have also been proposed, including that prosociality is pursued for its stress-mitigating effects (von Dawans et al., 2012; Harbaugh et al., 2007) or that it may occur due to increased impulsivity following acute stress (Yousseff et al., 2012).

Results from our analysis of autonomic, endocrine, and subjective measures of stress reactivity suggest that increased altruism following acute stress cannot be explained by differences in stress reactivity. Neither autonomic nor cortisol reactivity was associated with donation behavior, consistent with the majority of past studies in adults (von Dawans et al., 2012, 2019; Steinbeis et al., 2015). Similarly, our exploratory analysis found no relation between participant-reported subjective stress and donation behavior. In addition, while controlling for either biological or subjective stress measures during the TSST-M, the effect of condition on donation amount remained significant. Future research could benefit from assessing stress-induced changes in additional neurobiological markers implicated in altruism, such as oxytocin (Heinrichs & Domes, 2008) or brain activity in the mesolimbic-striatal brain region (Moll et al., 2006; Zaki & Mitchell, 2016), to help clarify the biological mediators for this effect. Future studies could also benefit from including an alone non-stress condition, in addition to the parent present nonstress condition utilized in the current study. This would facilitate disentangling the effects of being alone for 10 min from those of the subsequent stressor, thus testing the possibility that the alone condition is socially isolating and may be driving these effects independently of the stressor. Debriefing interviews with children could also be added in future research to probe children's motivations and cognitions during the donation task, and ask them whether they retained their "extra earnings" to share with their parent in the parent condition.

While we did not observe associations between stress reactivity and altruistic behavior, we did find evidence that trait-level individual differences in CAB predicted altruistic behavior. Specifically, we found that baseline CAB showed a negative quadratic relation with donation amount, such that baseline CAB values closer to zero predicted increased donation amount compared with greater absolute values (i.e., high negative or high positive values). These findings are consistent with recent evidence that autonomic indices can exhibit inverse U-shaped associations with altruism and general prosocial behavior (Kogan et al., 2014; Miller et al., 2017; Zhang & Wang, 2019). Past findings have been limited to single branch measures of the ANS, primarily focusing on parasympathetic activity (e.g., RSA); the current study expanded upon this by looking at dual-branch measures of autonomic activity. There is increasing interest in autonomic balance derived from simultaneous recordings of PEP and RSA (Quigley & Moores, 2018). Our findings are the first to highlight the utility of CAB, derived from simultaneous recordings of the parasympathetic and sympathetic activities, in understanding individual differences in children's altruism.

An inverse U-shaped relation between baseline CAB and altruism, with a peak near zero, suggests that greater altruistic behavior is predicted by balance of the two ANS branches. These findings may Developmental Science

be explained in a similar manner as previously observed relations between moderate and flexible parasympathetic activity and greater prosociality (Miller, 2018). A physiological profile characterized by high parasympathetic and low sympathetic activity (i.e., high CAB) may prevent a person from attending to and recognizing distress in others. On the other hand, a physiological profile characterized by low parasympathetic and high sympathetic activity (i.e., low CAB) may predispose an individual toward overreactions during challenging social situations, interfering with the process of directing internal resources toward others. Balance between these two systems may help someone react just enough to facilitate engagement, without becoming overwhelmed. Hastings et al. had previously hypothesized that moderate coactivation of both ANS branches could be associated with greater prosociality (2014); the current study is the first to provide evidence in support of this hypothesis.

Interestingly, the inclusion of baseline CAB in the models increased the effect size estimate for the effect of acute stress on donation behavior, suggesting that the effect of acute stress on altruism may be more easily detected once we account for individual differences in trait-level autonomic physiology. Trait-level autonomic physiology may represent an important foundation upon which differences in altruistic responding to threat develop. For instance, children with moderate baseline ANS activity may be more amenable to socialization processes that encourage them to display an altruistic response under stress.

Consistent with the notion that altruism is shaped by socialization processes, we found that donation behavior was positively associated with child age. This is consistent with substantial evidence from past studies showing that older children tend to exhibit more prosocial behavior compared with younger children (Fehr et al., 2008; Li et al., 2013; Miller et al., 2016; Sutter & Kocher, 2007). We did not find a significant relation between sex and altruism, which is in contrast to some studies documenting greater prosociality in girls compared with boys (Krevans & Gibbs, 1996; Miller et al., 2015, 2016). It has been suggested that sex differences in prosociality may be stronger when self or other-reported, compared with when observed behaviorally (Hastings et al., 2005), and may be stronger when the prosocial behavior is public, compared with anonymous (Carlo et al., 2003), potentially reflecting societal expectations for gender norms (Clarke-Stewart & Parke, 2014). The altruism measure in the current study was behavioral and the participant was alone during the donation task, which may explain why no main effect of sex was observed.

This study contributes important evidence toward a more complete understanding of human social behavior following acute stress exposure. However, there are some limitations that future studies should address. Firstly, this study may be limited by its relatively high SES sample. Previous studies have documented SES-altruism associations using either family income (Miller et al., 2015) or parental education level (van Ijzendoorn et al., 2010). It is possible that the lack of a relation between family income and altruism in the current study is due to the low variability within our sample of primarily middle to higher SES children. Future studies could benefit from testing tend-and-befriend behavior within a more diverse sample of children.

In addition, our results may be limited by our study design, which lacked more fine-grained CAB data within the altruism task. By turning off the camera during the altruism task, we were unable to separate RSA and PEP activity during the empathy induction period (i.e., story about sick children) from the donation decision period to investigate ANS activity changes during the task. While turning the camera off was important for reducing social desirability bias, future studies could benefit from having the children press a button after the empathy induction narrative and after the donation decision occurs. The use of a computer program for donation behavior could be employed for this purpose; however, this could potentially reduce ecological validity.

Lastly, our results may be limited by our age range. Previous research has found that parental support is less effective at buffering stress reactivity among adolescents as compared to children (Hostinar et al., 2015). It is therefore possible that the current results may not generalize to older youths. Future research should replicate these findings with a sample that includes both children and adolescents to directly test moderation by age or pubertal status. Future research with an adolescent sample could also benefit from testing how peer support might influence the effect of stress on altruism.

Despite these limitations, this study has several strengths. This is the first study to document "tend-and-befriend" behavior in children using random assignment to acute stress exposure. The examination of sex differences also contributes novel information. This study also utilized an altruism paradigm with high ecological validity; being asked to donate or share money is a situation that children may find themselves in during their normal lives. In addition, this was the first study to investigate the influence of CAB on donation behavior. Although more research is needed to fully elucidate the biological and cognitive mechanisms involved, this study adds to existing evidence that differential autonomic activity at rest may predict altruistic behavior in various contexts and highlights the added value of testing quadratic relations between physiology and behavior and incorporating indices of both ANS branches in socialemotional research. Considering the health and psychological benefits of altruism (Benson et al., 2007), a comprehensive understanding of the individual and contextual level predictors of altruistic behavior among children is an important goal for developmental science. More specifically, an altruistic stress response in children may have important implications for treating stress disorders or mitigating the deleterious effects of acute stress. For example, providing children with opportunities for prosocial engagement following stressful situations may take advantage of inherent "tend-and-befriend" tendencies, resulting in better coping. Observing altruistic responding to stress in childhood suggests this is a developmental period when altruism could potentially be nurtured and promoted. Considering the societal consequences of individual decisions to either band together or remain self-focused during times of national or global threat, a better understanding of altruism during threat is of great societal value.

ACKNOWLEDGMENTS

CEH was supported by a National Institute of Health grant R01 HD093898 (PI Bitler) while working on this manuscript. The first author (NVA) was supported by the Dean's Distinguished Graduate Fellowship (DDGF) provided by the University of California, Davis. The authors would like to thank Anna M. Parenteau, Adam T. Nissen, and Jennifer La for their valuable contributions to this study.

CONFLICT OF INTEREST

The authors report no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Paul D. Hastings D https://orcid.org/0000-0003-2978-7364 Camelia E. Hostinar D https://orcid.org/0000-0001-8703-3347

REFERENCES

- Alen, N. V., Deer, L. K., & Hostinar, C. E. (2020). Autonomic nervous system activity predicts increasing serum cytokines in children. *Psychoneuroendocrinology*, 119, 104745. https://doi.org/10.1016/j. psyneuen.2020.104745.
- Apter-Levi, Y., Pratt, M., Vakart, A., Feldman, M., Zagoory-Sharon, O., & Feldman, R. (2016). Maternal depression across the first years of life compromises child psychosocial adjustment; relations to child HPA-axis functioning. *Psychoneuroendocrinology*, 64, 47–56. https://doi.org/10.1016/j.psyneuen.2015.11.006.
- Bavel, J. J. V., Baicker, K., Boggio, P. S., Capraro, V., Cichocka, A., Cikara, M., Crockett, M. J., Crum, A. J., Douglas, K. M., Druckman, J. N., Drury, J., Dube, O., Ellemers, N., Finkel, E. J., Fowler, J. H., Gelfand, M., Han, S., Haslam, S. A., Jetten, J., ... Willer, R. (2020). Using social and behavioural science to support COVID-19 pandemic response. *Nature Human Behaviour*, *4*, 460–471. https://doi.org/10.1038/ s41562-020-0884-z.
- Beauchaine, T. P., Gatzke-Kopp, L., & Mead, H. K. (2007). Polyvagal theory and developmental psychopathology: Emotion dysregulation and conduct problems from preschool to adolescence. *Biological Psychology*, 74(2), 174–184. https://doi.org/10.1016/j.biops ycho.2005.08.008.
- Benson, P. L., Clary, E. G., & Scales, P. C. (2007). Altruism and health: Is there a link during adolescence? In Post, S. G. (Ed.), Altruism and health: Perspectives from empirical research; altruism and health: Perspectives from empirical research (pp. 97–115, Chapter xxii, 458 Pages) : Oxford University Press. https://doi.org/10.1093/acpro f:oso/9780195182910.003.000.
- Berntson, G. G., Cacioppo, J. T., & Quigley, K. S. (1991). Autonomic determinism: The modes of autonomic control, the doctrine of autonomic space, and the laws of autonomic constraint. *Psychological Review*, 98(4), 459–487. https://doi.org/10.1037/0033295X.98.4.459.
- Berntson, G. G., Lozano, D. L., Chen, Y., & Cacioppo, J. T. (2004). Where to Q in PEP. *Psychophysiology*, 41(2), 333–337. https://doi. org/10.1111/j.1469-8986.2004.00156.x.
- Berntson, G. G., Norman, G. J., Hawkley, L. C., & Cacioppo, J. T. (2008). Cardiac autonomic balance versus cardiac regulatory capacity. *Psychophysiology*, 45(4), 643–652. https://doi. org/10.1111/j.1469-8986.2008.00652.x.
- Berntson, G. G., Thomas bigger, J., Eckberg, D. L., Grossman, P., Kaufmann, P. G., Malik, M., Nagaraja, H. N., Porges, S. W., Saul, J. P.,

Developmental Science

Stone, P. H., & Van der molen, M. W. (1997). Heart rate variability: Origins, methods, and interpretive caveats. *Psychophysiology*, *34*(6), 623–648.

- Brett, B. E. (2017). The effect of supportive social interaction priming on children's prosocial comforting responses to distressed others (Unpublished doctoral dissertation). University of Maryland. Retrieved from https://search.proquest.com/docview/19246 33571?accountid=14496.
- Brown, S. L., Fredrickson, B. L., Wirth, M. M., Poulin, M. J., Meier, E. A., Heaphy, E. D., Cohen, M. D., & Schultheiss, O. C. (2009). Social closeness increases salivary progesterone in humans. *Hormones* and Behavior, 56, 108–111.
- Bubier, J. L., Drabick, D. A. G., & Breiner, T. (2009). Autonomic functioning moderates the relations between contextual factors and externalizing behaviors among inner-city children. *Journal* of Family Psychology, 23(4), 500–510. https://doi.org/10.1037/ a0015555.
- Bulmer, M. G. (1979). Principles of statistics (Dover). Dover.
- Bylsma, L. M., Yaroslavsky, I., Rottenberg, J., Jennings, J. R., George, C. J., Kiss, E., Kapornai, K., Halas, K., Dochnal, R., Lefkovics, E., Benák, I., Baji, I., Vetró, Á., & Kovacs, M. (2015). Juvenile onset depression alters cardiac autonomic balance in response to psychological and physical challenges. *Biological Psychology*, 110, 167–174. https://doi. org/10.1016/j.biopsycho.2015.07.003.
- Cannon, W. B. (1932). The wisdom of the body. W. W. Norton & Company Inc.
- Carlo, G., Hausmann, A., Christiansen, S., & Randall, B. A. (2003). Sociocognitive and behavioral correlates of a measure of prosocial tendencies for adolescents. *The Journal of Early Adolescence*, 23(1), 107–134. https://doi.org/10.1177/0272431602239132.
- Cauce, A. M., Mason, C., Gonzales, N., Hiraga, Y., & Liu, G. (1994). Social support during adolescence: Methodological and theoretical considerations. In F. Nestmann, & K. Hurrelmann (Eds.), Social networks and social support in childhood and adolescence; social networks and social support in childhood and adolescence (pp. 89–108, Chapter xii, 441 Pages) Oxford, England: Walter De Gruyter.
- Clark, C. A. C., Skowron, E. A., Giuliano, R. J., & Fisher, P. A. (2016). Intersections between cardiac physiology, emotion regulation and interpersonal warmth in preschoolers: Implications for drug abuse prevention from translational neuroscience. *Drug and Alcohol Dependence*, *163*, S60–S69. https://doi.org/10.1016/j.druga lcdep.2016.01.033.
- Clarke-Stewart, A., & Parke, R. D. (2014). Social development (2nd edn.). John Wiley & Sons.
- Cohen, J. R., Thomsen, K. N., Tu, K. M., Thakur, H., McNeil, S., & Menon, S. V. (2020). Cardiac autonomic functioning and post-traumatic stress: A preliminary study in youth at-risk for PTSD. *Psychiatry Research*, 284, 8. https://doi.org/10.1016/j.psychres.2019.112684.
- de Guzman, M., Rosario, T., Jung, E., & Anh, D. K. (2012). Perceived social support networks and prosocial outcomes among Latino/a youth in the United States. *Revista Interamericana De Psicología*, 46(3), 413– 424.Retrieved from https://search.proquest.com/docview/14493 08741?accountid=14505.
- Diamond, L. M., & Cribbet, M. R. (2013). Links between adolescent sympathetic and parasympathetic nervous system functioning and interpersonal behavior over time. *International Journal of Psychophysiology*, 88(3), 339–348. https://doi.org/10.1016/j.ijpsy cho.2012.08.008.
- Eisenberg, N., Fabes, R. A., Murphy, B., Karbon, M., Smith, M., & Maszk, P. (1996). The relations of children's dispositional empathy-related responding to their emotionality, regulation, and social functioning. *Developmental Psychology*, 32(2), 195–209. https://doi.org/10.1037 /0012-1649.32.2.195.
- Enders, C. K., & Bandalos, D. L. (2001). The relative performance of full information maximum likelihood estimation for missing data in

structural equation models. *Structural Equation Modeling*, 8(3), 430–457. https://doi.org/10.1207/S15328007SEM0803.

Ensor, R., & Hughes, C. (2010). With a little help from my friends: Maternal social support, via parenting, promotes willingness to share in preschoolers born to young mothers. *Infant and Child Development*, 19(2), 127–141.Retrieved from https://search.proquest.com/docvi ew/742980351?accountid=14496.

Fehr, E., Bernhard, H., & Rockenbach, B. (2008). Egalitarianism in young children. Nature, 454(7208), 1079–1083. https://doi.org/10.1038/ nature07155.

- Gunnar, M. R., & Hostinar, C. E. (2015). The social buffering of the hypothalamic-pituitary-adrenocortical axis in humans: Developmental and experiential determinants. Social Neuroscience, 10(5), 479–488. https://doi.org/10.1080/17470919.2015.1070747.
- Harbaugh, W. T., Mayr, U., & Burghart, D. R. (2007). Neural responses to taxation and voluntary giving reveal motives for charitable donations. *Science*, 316(5831), 1622–1625. https://doi.org/10.1126/ science.1140738.
- Hastings, P. D., Miller, J. G., Kahle, S., & Zahn-Waxler, C. (2014). The neurobiological bases of empathic concern for others. In M. Killen, & J. G. Smetana (Eds.), *Handbook of moral development* (2nd ed., pp. 411–434, Chapter xxv, 571 Pages). Psychology Press. https://doi.org/10.4324/9780203581957.ch19
- Hastings, P. D., Miller, J. G., & Troxel, N. R. (2015). Making good: The socialization of children's prosocial development. In J. E. Grusec & P. D. Hastings (Eds.), *Handbook of socialization: Theory and research* (pp. 637–660). New York, NY: Guilford Press.
- Hastings, P. D., Nuselovici, J. N., Utendale, W. T., Coutya, J., McShane, K. E., & Sullivan, C. (2008). Applying the polyvagal theory to children's emotion regulation: Social context, socialization, and adjustment. *Biological Psychology*, 79(3), 299–306. https://doi.org/10.1016/j. biopsycho.2008.07.005.
- Hastings, P. D., Rubin, K. H., & DeRose, L. (2005). Links among gender, inhibition, and parental socialization in the development of prosocial behavior. *Merrill-Palmer Quarterly*, *51*(4), 467–493. https://doi. org/10.1353/mpq.2005.0023.
- Hein, G., Lamm, C., Brodbeck, C., & Singer, T. (2011). Skin conductance response to the pain of others predicts later costly helping. *PLoS* One, 6(8), e22759. https://doi.org/10.1371/journal.pone.0022759.
- Heinrichs, M., & Domes, G. (2008). Neuropeptides and social behavior: Effects of oxytocin and vasopressin in humans. *Progress in Brain Research*, 170, 337–350.
- Hennessy, M. B., Kaiser, S., & Sachser, N. (2009). Social buffering of the stress response: Diversity, mechanisms, and functions. Frontiers in Neuroendocrinology, 30(4), 470–482. https://doi.org/10.1016/j. yfrne.2009.06.001.
- Holmgren, R. A., Eisenberg, N., & Fabes, R. A. (1998). The relations of children's situational empathy-related emotions to dispositional prosocial behaviour. *International Journal of Behavioral Development*, 22(1), 169–193. https://doi.org/10.1080/016502598384568.
- Hostinar, C. E., Johnson, A. E., & Gunnar, M. R. (2015). Parent support is less effective in buffering cortisol stress reactivity for adolescents compared to children. *Developmental Science*, 18(2), 281–297. https://doi.org/10.1111/desc.12195.
- Hostinar, C. E., Sullivan, R. M., & Gunnar, M. R. (2014). Psychobiological mechanisms underlying the social buffering of the hypothalamicpituitary-adrenocortical axis: A review of animal models and human studies across development. *Psychological Bulletin*, 140(1), 256-282. https://doi.org/10.1037/a0032671.
- Kalvin, C. B., Bierman, K. L., & Gatzke-Kopp, L. (2016). Emotional reactivity, behavior problems, and social adjustment at school entry in a high-risk sample. *Journal of Abnormal Child Psychology*, 44(8), 1527– 1541. https://doi.org/10.1007/s10802-016-0139-7.
- Kirschbaum, C., Pirke, K., & Hellhammer, D. H. (1993). The "trier social stress test": A tool for investigating psychobiological stress

responses in a laboratory setting. *Neuropsychobiology*, 28(1–2), 76–81. https://doi.org/10.1159/000119004.

- Kogan, A., Oveis, C., Carr, E. W., Gruber, J., Mauss, I. B., Shallcross, A., Impett, E. A., van der Lowe, I., Hui, B., Cheng, C., & Keltner, D. (2014). Vagal activity is quadratically related to prosocial traits, prosocial emotions, and observer perceptions of prosociality. *Journal* of Personality and Social Psychology, 107(6), 1051–1063. https://doi. org/10.1037/a0037509.
- Krevans, J., & Gibbs, J. C. (1996). Parents' use of inductive discipline: Relations to children's empathy and prosocial behavior. *Child Development*, 67(6), 3263–3277. https://doi. org/10.2307/1131778.
- Laborde, S., Mosley, E., & Thayer, J. F. (2017). Heart rate variability and cardiac vagal tone in psychophysiological research— Recommendations for experiment planning, data analysis, and data reporting. *Frontiers in Psychology*, 8(February), 1–18. https://doi. org/10.3389/fpsyg.2017.00213
- Lambe, L. J., Craig, W. M., & Hollenstein, T. (2019). Blunted physiological stress reactivity among youth with a history of bullying and victimization: Links to depressive symptoms. Journal of Abnormal Child Psychology, 47(12), 1981–1993. https://doi.org/10.1007/s10802-019-00565-y.
- Li, Y., Li, H., Decety, J., & Lee, K. (2013). Experiencing a natural disaster alters children's altruistic giving. Psychological Science, 24(9), 1686– 1695. https://doi.org/10.1177/0956797613479975.
- Lozano, D. L., Norman, G., Knox, D., Wood, B. L., Miller, B. D., Emery, C. F., & Berntson, G. G. (2007). Where to B in dZ/dt. *Psychophysiology*, 44(1), 113–119. https://doi.org/10.1111/j.1469-8986.2006.00468.x.
- Miller, J. G. (2018). Physiological mechanisms of prosociality. Current Opinion in Psychology, 20, 50–54. https://doi.org/10.1016/j. copsyc.2017.08.018.
- Miller, J. G., & Hastings, P. D. (2016). Biopsychosocial models of prosociality: Compassionate love, vagal regulation, and children's altruism.
 In D. Narvaez, J. M. Braungart-Rieker, L. E. Miller-Graff, L. T. Gettler, & P. D. Hastings (Eds.), Contexts for young child flourishing: Evolution, family, and society; contexts for young child flourishing: Evolution, family, and society (pp. 185–200, Chapter xiv, 369 Pages) : Oxford University Press. https://doi.org/10.1093/acprof:oso/9780190237 790.003.0009.
- Miller, J. G., Kahle, S., & Hastings, P. D. (2015). Roots and benefits of costly giving: Children who are more altruistic have greater autonomic flexibility and less family wealth. *Psychological Science*, 26(7), 10381045. https://doi.org/10.1177/0956797615578476.
- Miller, J. G., Kahle, S., & Hastings, P. D. (2017). Moderate baseline vagal tone predicts greater prosociality in children. *Developmental Psychology*, 53(2), 274–289. https://doi.org/10.1037/dev0000238.
- Miller, J. G., Nuselovici, J. N., & Hastings, P. D. (2016). Nonrandom acts of kindness: Parasympathetic and subjective empathic responses to sadness predict children's prosociality. *Child Development*, 87(6), 1679–1690. https://doi.org/10.1111/cdev.12629.
- Miller, J. W., Stromeyer, W. R., & Schwieterman, M. A. (2013). Extensions of the johnson-neyman technique to linear models with curvilinear effects: Derivations and analytical tools. *Multivariate Behavioral Research*, 48(2), 267–300. https://doi.org/10.1080/00273 171.2013.763567.
- Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. (2006). Human fronto-mesolimbic networks guide decisions about charitable donation. PNAS Proceedings of the National Academy of Sciences of the United States of America, 103(42), 15623– 15628. https://doi.org/10.1073/pnas.060447510.
- Ochi, M., & Fujiwara, T. (2016). Association between parental social interaction and behavior problems in offspring: A population-based study in japan. *International Journal of Behavioral Medicine*, 23(4), 447-457. https://doi.org/10.1007/s12529-015-9532-9.
- Parenteau, A. M., Alen, N. V., Deer, L. K., Nissen, A., Luck, A. T., & Hostinar, C. E. (2021). Parenting matters: Parents can reduce or

amplify children's anxiety and cortisol responses to acute stress. Development and Psychopathology, 32, 1799–1809.

- Porges, S. W. (2007). The polyvagal perspective. Biological Psychology, 74(2), 116–143. https://doi.org/10.1016/j.biopsycho.2006.06.009.
- Potts, S. R., McCuddy, W. T., Jayan, D., & Porcelli, A. J. (2019). To trust, or not to trust? Individual differences in physiological reactivity predict trust under acute stress. *Psychoneuroendocrinology*, 100, 75– 84. https://doi.org/10.1016/j.psyneuen.2018.09.019.
- Quigley, K. M., & Moore, G. A. (2018). Development of cardiac autonomic balance in infancy and early childhood: A possible pathway to mental and physical health outcomes. *Developmental Review*, 49, 41–61. https://doi.org/10.1016/j.dr.2018.06.004.
- Shader, T. M., Gatzke-Kopp, L. M., Crowell, S. E., Jamila Reid, M., Thayer, J. F., Vasey, M. W., Webster-Stratton, C., Bell, Z., & Beauchaine, T. P. (2018). Quantifying respiratory sinus arrhythmia: Effects of misspecifying breathing frequencies across development. *Development* and Psychopathology, 30(1), 351–366. https://doi.org/10.1017/ S0954579417000669.
- Sherwood(Chair), A., Allen, M. T., Fahrenberg, J., Kelsey, R. M., Lovallo, W. R., & Doornen, L. J. P. (1990). Methodological guidelines for impedance cardiography. Psychophysiology, 27, 1–23.
- Simons, S. S. H., Cillessen, A. H. N., & de Weerth, C. (2017). Cortisol stress responses and children's behavioral functioning at school. *Developmental Psychobiology*, 59(2), 217–224. https://doi.org/10.1002/dev.21484.
- Singer, N., Sommer, M., Döhnel, K., Zänkert, S., Wüst, S., & Kudielka, B. M. (2017). Acute psychosocial stress and everyday moral decisionmaking in young healthy men: The impact of cortisol. *Hormones and Behavior*, 93, 72–81. https://doi.org/10.1016/j.yhbeh.2017.05.002.
- Sollberger, S., Bernauer, T., & Ehlert, U. (2016). Stress influences environmental donation behavior in men. *Psychoneuroendocrinology*, 63, 311–319. https://doi.org/10.1016/j.psyneuen.2015.10.017.
- Steinbeis, N., Engert, V., Linz, R., & Singer, T. (2015). The effects of stress and affiliation on social decision-making: Investigating the tendand-befriend pattern. *Psychoneuroendocrinology*, *62*, 138–148. https://doi.org/10.1016/j.psyneuen.2015.08.003.
- Stewart, D., & Sun, J. (2004). How can we build resilience in primary school aged children? The importance of social support from adults and peers in family, school and community settings. Asia-Pacific Journal of Public Health, 16, S37–S41. Retrieved from https://search. proquest.com/docview/620725123?accountid=14496.
- Sutter, M., & Kocher, M. G. (2007). Trust and trustworthiness across different age groups. Games and Economic Behavior, 59(2), 364–382. https://doi.org/10.1016/j.geb.2006.07.006.
- Taylor, S. E. (2006). Tend and befriend: Biobehavioral bases of affiliation under stress. Current Directions in Psychological Science, 15, 273– 277. https://doi.org/10.1111/j.1467-8721.2006.00451.x.
- Taylor, S. E., Klein, L. C., Lewis, B. P., Gruenewald, T. L., Gurung, R. A., & Updegraff, J. A. (2000). Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review*, 107, 411–429.
- Tiffany, K. (2020). The hand-sanitizer Hawkers aren't sorry. The Atlantic. https://www.theatlantic.com/health/archive/2020/03/hand-sanit izer-online-sales-ebay-craigslist-price-surge/607750/.
- Tomova, L., Majdandžić, J., Hummer, A., Windischberger, C., Heinrichs, M., & Lamm, C. (2017). Increased neural responses to empathy for pain might explain how acute stress increases prosociality. *Social Cognitive and Affective Neuroscience*, 12(3), 401–408.
- van Ijzendoorn, M. H., Bakermans-Kranenburg, M., Pannebakker, F., & Out, D. (2010). In defence of situational morality: Genetic, dispositional and situational determinants of children's donating to charity. *Journal of Moral Education*, 39(1), 1–20. https://doi. org/10.1080/03057240903528535.
- Vinkers, C. H., Zorn, J. V., Cornelisse, S., Koot, S., Houtepen, L. C., Olivier, B., Verster, J. C., Kahn, R. S., Boks, M. P. M., Kalenscher, T., & Joëls, M. (2013). Time-dependent changes in altruistic punishment following stress. *Psychoneuroendocrinology*, *38*(9), 1467–1475. https:// doi.org/10.1016/j.psyneuen.2012.12.012.

- von Dawans, B., Ditzen, B., Trueg, A., Fischbacher, U., & Heinrichs, M. (2019). Effects of acute stress on social behavior in women. *Psychoneuroendocrinology*, 99, 137–144. https://doi.org/10.1016/j. psyneuen.2018.08.031.
- von Dawans, B., Fischbacher, U., Kirschbaum, C., Fehr, E., & Heinrichs, M. (2012). The social dimension of stress reactivity: Acute stress increases prosocial behavior in humans. *Psychological Science*, 23(6), 651–660. https://doi.org/10.1177/0956797611431576.
- von Dawans, B., Trueg, A., Kirschbaum, C., Fischbacher, U., & Heinrichs, M. (2018). Acute social and physical stress interact to influence social behavior: The role of social anxiety. *PLoS One*, 13(10), 21, e0204665.
- Yim, I. S., Quas, J. A., Cahill, L., & Hayakawa, C. M. (2010). Children's and adults' salivary cortisol responses to an identical psychosocial laboratory stressor. *Psychoneuroendocrinology*, 35(2), 241–248. https:// doi.org/10.1016/j.psyneuen.2009.06.014.
- Youssef, F. F., Dookeeram, K., Basdeo, V., Francis, E., Doman, M., Mamed, D., Maloo, S., Degannes, J., Dobo, L., Ditshotlo, P., & Legall, G. (2012). Stress alters personal moral decision making. *Psychoneuroendocrinology*, 37(4), 491–498. https://doi. org/10.1016/j.psyneuen.2011.07.017.
- Zaki, J., & Mitchell, J. P. (2016). Prosociality as a form of reward seeking. In J. D. Greene, I. Morrison, & M. E. P. Seligman (Eds.), *Positive*

neuroscience (pp. 57-72, Chapter x, 241 Pages). : Oxford University Press.

Zhang, R., & Wang, Z. (2019). The mediating effect of empathy in the quadratic relationship between children's resting RSA and sharing behavior. *International Journal of Psychophysiology*, 140, 8–14. https://doi.org/10.1016/j.ijpsycho.2019.03.012.

SUPPORTING INFORMATION

Developmental Science

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Alen NV, Deer LK, Karimi M, Feyzieva E, Hastings PD, Hostinar CE. Children's altruism following acute stress: The role of autonomic nervous system activity and social support. *Dev Sci.* 2021;00:e13099. <u>https://</u> doi.org/10.1111/desc.13099