Title
Prosocially-Motivated Learning from Childhood to Young Adulthood: A Cross-Sectional Examination of Neurocomputational Mechanisms and Antiviral Correlates

Author
Leschak, Carrianne Janine

Publication Date
2021

UNIVERSITY OF CALIFORNIA

Los Angeles

Prosocially-Motivated Learning from Childhood to Young Adulthood: A Cross-Sectional Examination of Neurocomputational Mechanisms and Antiviral Correlates

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Psychology

by

Carrianne Janine Leschak

2021

ABSTRACT OF THE DISSERTATION

Prosocially-Motivated Learning from Childhood to Young Adulthood:

A Cross-Sectional Examination of

Neurocomputational Mechanisms and Antiviral Correlates

by

Carrianne Janine Leschak

Doctor of Philosophy in Psychology

University of California, Los Angeles, 2021

Professor Naomi Ilana Eisenberger, Chair

Despite mounting evidence that prosocial behavior is related to positive health outcomes, current understanding of prosocial neurodevelopment is limited. However, particular features of adolescent development (e.g., increases in perspective-taking, focus on peers) may facilitate prosocial behavior during adolescence, especially toward friends. The present work examines prosocial neurodevelopment from childhood through young adulthood by utilizing a reinforcement learning framework to assess prosocial behavior toward a friend. Participants (9-20 years old) completed self-report measures of empathy and selected a close friend. They then completed a multi-part reinforcement learning paradigm, including a) a learning phase while undergoing a functional magnetic resonance imaging scan, where performance was related to monetary outcomes for either the participant (self learning) or the selected friend (prosocial

learning), b) a test phase to assess learning, and c) a surprise memory test to examine episodic memory to reinforcement events. A subset of participants completed a blood draw to assess the IFN-γ, a cytokine related to antiviral immunity, a week later. Prosocial learning accuracy tended to peak in mid-adolescence, while the trajectory across age for self learning plateaued starting in early adolescence. Although children performed worse in terms of learning accuracy relative to other age groups, they had better episodic memory for the reinforcement events during learning. Hippocampal activity during learning was negatively associated with age and positively correlated with performance on the memory task, in line with the past work showing that the hippocampus plays a major role in memory. In females, empathy was differentially associated with prosocial learning performance across age, such that greater empathy was linked to worse prosocial learning accuracy in young adult females. This counterintuitive finding may reflect increased behavioral reactivity to other-relevant feedback in highly empathic individuals, leading to more volatile behavior and thus worse overall performance. No differences in neural activity were found with respect to prosocial vs. self learning. The subtlety of the manipulation may have contributed to the observed null results for comparisons between prosocial vs self learning in the present study. IFN-γ was not significantly related to any study outcomes.

The dissertation of Carrianne Janine Leschak is approved.

Andrew J. Fuligni

Adriana Galván

Theodore Francisco Robles

Naomi Ilana Eisenberger, Committee Chair

University of California Los Angeles

2021

Table of Contents

Lists of Tables

Lists of Figures

List of Supplementary Material

Acknowledgements

I would like to thank my committee members, Drs. Eisenberger, Fuligni, Galván, and Robles for their incredible feedback, guidance, and support on this line of work. I am grateful that Drs. Eisenberger, Fuligni, and Galván entrusted me with this project as a young graduate student. I am immensely grateful for the fellow graduate students, undergraduate research assistants, and project coordinators who assisted in the organization and data collection for this project, as well as the feedback and support that I received from the Social and Affective Neuroscience (SAN) Laboratory throughout this research and my graduate career.

Several peers and colleagues have been instrumental in my growth as both a scientist and a person throughout my graduate career and I could not be more thankful to have been surrounded by such brilliant and kind people. I would especially like to thank Jessica Shropshire who constantly reminded me the importance of self-care, built me up during challenging times, and always provided unwavering support. I would also like to express my gratitude for Kate Byrne Haltom, whose incredible work ethic, attention to detail, and selfless generosity not only contributed to my successes, but also provided an incredible role model to look up to on a daily basis.

I would also like to thank my undergraduate research advisor, Dr. Richard Pond, whose early guidance and research training led me to attend UCLA for graduate school.

Outside of academia, I am incredibly lucky to have such supportive family and friends. I am forever grateful to my parents for whole-heartedly supporting my move to the other side of the country, and continuing to provide remote emotional and instrumental support throughout my studies. I would be remiss if I did not acknowledge the emotional support of my canine

companion, Trooper, who listened intently to countless practice talks and was a joyous reminder of the importance of work-life balance throughout the second half of graduate school.

Finally, this research was supported by generous funding from the UCLA Dissertation Year Fellowship and the National Institute of Health.

Vita

EDUCATION

2016	M.A., Psychology; University of California, Los Angeles
2015	B.A., Psychology, Sociology, Criminology *Summa Cum Laude*; University of North Carolina Wilmington

SELECTED FUNDING

2020-2021	Dissertation Year Fellowship, UCLA
2020	Elizabeth Blackwell, MD, Graduate Award, UCLA
2019-2021	NIH National Research Service Award, F31 Predoctoral Fellowship
2019-20	Clara Leplin & Beatrice Rasof Fellowship, Department of Psychology, UCLA
2018-2019	NIH National Research Service Award, T32 Predoctoral Fellowship
2016	Graduate Summer Research Mentorship Award, UCLA
2015-16	Irving and Jean Stone Fellowship, UCLA
2015-16	Distinguished University Fellowship, UCLA

PUBLICATIONS

Leschak, C. J., Dutcher, J. M., Haltom, K. E. B., Breen, E. C., Bower, J. E., & Eisenberger, N. I. (2020). Associations between amygdala reactivity to social threat, perceived stress, and C-reactive protein in breast cancer survivors. *Social Cognitive and Affective Neuroscience*.

Leschak, C. J. & Eisenberger, N. I. (2019). Two distinct immune pathways linking social relationships with health: Inflammatory and antiviral processes. *Psychosomatic Medicine*.

Leschak, C. J. & Eisenberger, N. I. (2018). The role of social relationships in the link between olfactory dysfunction and mortality. *PLoS One*.

Leschak, C. J. & Eisenberger, N. I. (2016). Social pain/hurt. In V. Zeigler-Hill & T. K. Shackelford (Eds.), *Encyclopedia of Personality and Individual Differences*. Springer International Publishing.

ORAL PRESENTATIONS

Prosocially-motivated learning during adolescence: Neurocomputational mechanisms and antiviral correlates. Invited talk presented at the Brain & Behavioral Development During Adolescence (BBDA) Lecture Series, UCLA. (March 6, 2020)

Neural mechanisms of prosocial learning across development. Invited talk presented at the Brain & Behavioral Development During Adolescence (BBDA) Lecture Series, UCLA. (March 1, 2019)

SELECTED CONFERENCE POSTER PRESENTATIONS

Karan, M., Lazar, L., Cooper-White, M., Eisenberger, N. I., Galván, A., Leschak, C. J., Telzer, E. H., Uy, J. P., Fuligni, A. J. (2020, September). *The neurodevelopment of prosocial behavior in adolescence*. Poster to be presented at the Flux Virtual Congress.

Wang†, Z., Leschak, C. J., Dutcher, J. M., Haltom, K. E. B., Bower, J. E., & Eisenberger, N. I. (2020, May). *Associations between social support and neural responses to prosocial behaviors in breast cancer survivors*. Poster presented at the Undergraduate Research Showcase, UCLA, Los Angeles, CA.

Uy, J. P., Cooper-White, M., Leschak, C. J., Eisenberger, N. I., Fuligni, A. J., Galván, A. (2019, September). *Adolescents exhibit dampened prefrontal activation to stress compared to children and adults*. Poster presented at the Flux Congress, The Society for Developmental Cognitive Neuroscience, New York, NY.

Teed, A. R., Leschak, C. J., Katzman, P. L., Irwin, M. R., Eisenberger, N. I., Lieberman, M. D., & Tabak, B. A. (2019, May). *The effects of oxytocin and vasopressin on neural processing of parents faces is dependent on perceived care from fathers but not mothers*. Poster presented at the 12th Annual Meeting of the Social and Affective Neuroscience Society (SANS), Miami, FL.

Leschak, C. J., Hornstein, E. A., Haltom, K. E. B., & Eisenberger, N. I. (2018, August). *Neural correlates of pathogen detection & avoidance: Perceived vulnerability to disease & behavioral avoidance of sick others*. Poster presented at the São Paulo School of Advanced Science on Social and Affective Neuroscience (SPSAN), Saõ Paulo, Brazil.

Odashima, A., Leschak, C. J., Dutcher, J. M., Haltom, K. E. B., Bower, J. E., Breen, E. C., Irwin, M. R., & Eisenberger, N. I. (2018, May). *Effects of giving and receiving support on inflammation and the moderating effect of stress*. Poster presented at Undergraduate Research Week Poster Day, UCLA, Los Angeles, CA.

Leschak, C. J., Dutcher, J. M., Haltom, K. E. B., Bower, J. E. & Eisenberger, N. I. (2018, May). *Rethinking the meaning of striatal activation: Ventral striatum activity during acute stress in females*. Poster presented at the 11th Annual Meeting of the Social and Affective Neuroscience Society (SANS), Brooklyn, NY.

Leschak, C. J., Dutcher, J. M., Haltom, K. E. B., Bower, J. E., Breen, E. C., Irwin, M. R., & Eisenberger, N. I. (2018, March). *Anti-viral implications for social connection: Circulating biomarker of anti-viral immunity (IFN-γ) is associated with degree of social connectedness*. Poster presented at the Health Psychology Preconference of the 19th Annual Society for Personality and Social Psychology (SPSP) Convention, Atlanta, GA.

SELECTED TEACHING POSITIONS

2020/2017	Teaching Associate, Introduction to Social Psychology, UCLA
2019	Teaching Associate, Leadership Foundation for MBA students, UCLA
2018	Co-Instructor, fMRI Training Course for the Social and Affective Neuroscience/ Social Cognitive Neuroscience Labs, UCLA
2018	Teaching Associate, Nonexperimental Methods in Social Psychology, UCLA
2017/2016	Teaching Assistant, Social Psychology Laboratory, UCLA

Prosocially-Motivated Learning in Children, Adolescents, and Young Adults: A Cross-Sectional Examination of Neurocomputational Mechanisms and Antiviral Correlates

I. Overview

The positive effect of social relationships on physical health has been of interest for decades, with a recent focus on underlying neural and immune mechanisms. One aspect of social relationships, prosocial behavior, or behavior that benefits another person, has been linked with positive health outcomes such as reduced proinflammatory profiles for those who engage in more frequent prosocial behavior (Nelson-Coffey et al., 2017). Thus, prosocial behavior may be one contributing factor to the observed link between social relationships and health, with modulated immune activity as a potential mechanism. A developmental examination across adolescence can help further elucidate how these relationships may unfold across early development alongside normative, maturational brain development.

However, trends in prosocial behavior from childhood to adolescence have not been clearly identified, partially due to divergent measurement approaches. Thus, the present study seeks to examine these developmental trends in prosocial behavior, and the underlying neural mechanisms, utilizing a reinforcement learning paradigm. Such paradigms allow us to examine incremental learning, or the trajectory of learning on a trial-by-trial basis. In addition, we can examine episodic memory for reinforcement events that occur on a trial level. These behavioral measures can then be associated with neural or self-reported individual difference measures, possibly shedding light on how specific components of prosocial learning may be linked with physical health outcomes.

Primary Aim

The overall goal of the present work is to examine the neurobehavioral mechanisms of prosocially-motivated learning (learning to benefit a friend, hereafter called prosocial learning), as compared to self-motivated learning (learning to benefit oneself), from adolescence to young adulthood, utilizing reinforcement learning paradigms to understand the development of prosocial motivation and behavior.

Exploratory Aim 1

Closely tied to the primary aim, the study population will include a younger age group, namely pre-adolescent children. Very little work has been done on the neural mechanisms of prosocial behavior prior to adolescence. Thus, the inclusion of children in the present work is a first step in understanding the emergence of prosocial behavior into adolescence.

Exploratory Aim 2

Recent work has highlighted that, in addition to inflammation, antiviral immunity may be a secondary mechanistic pathway in the bidirectional relationships between social factors and physical health, such that individuals with bolstered antiviral immunity may be more likely to engage in prosocial behavior, as they are more protected from viral pathogens that may be transmitted through social contact (Leschak & Eisenberger, 2019). An exploratory aim of the present work will be to examine associations between a circulating marker related to antiviral immunity (interferon-gamma, IFN-γ) and prosocial learning in a subsample of adolescents and young adults.

II. Background

A large body of empirical work has focused on the neural correlates of risky behavior and

mental disorders that emerge during adolescence, but knowledge of the neurobehavioral developments in prosocial behavior is quite limited (Crone & Dahl, 2012). The result is largely a portrait of adolescent brain development that focuses on risk and psychopathology over more positive behavior. The focus on risk and disorder is unfortunate because several prosocial behaviors that involve giving to others—ranging from volunteering to providing instrumental or social assistance—have been linked to healthy psychological, behavioral, and physical profiles, including lower mortality, fewer objective and subjective health problems, and lower depression, even during childhood and adolescence (Brown et al., 2003; Eisenberger, 2013; Eisenberger & Cole, 2012; Li & Ferraro, 2005; Miller et al., 2015; Morrow-Howell et al., 2003; Musick et al., 1999; Schreier et al., 2013; Van Goethem et al., 2014). Experimental studies in adolescents and adults have provided evidence for causality, showing that giving instrumental, financial, or social support to others can reduce cardiovascular risk factors and reduce individuals' response to threat and stressful events (Schreier et al., 2013; von Dawans et al., 2012).

The health benefits of giving to others warrant an increased focus on the neurobehavioral developments and mechanisms that underlie this core aspect of prosocial behavior during adolescence, a key point of development that can set the stage for lifelong health and well-being (Crone & Dahl, 2012; Falconi et al., 2014). Understanding the extent to which neural development may facilitate or inhibit giving to others can inform efforts to promote giving and prosocial behavior to enhance adolescent health and development, efforts which have recently become of increased interest (Van Goethem et al., 2014).

Clarifying Trends in Prosocial Development

In order to understand the role of neural development in prosocial behavior during adolescence, it is necessary to clarify the actual developmental differences in behavior. Decades

of study have yielded a curious pattern: Most research has found that prosocial behavior toward others increases starting around the preschool years (Eisenberg et al., 2015). However, this trend appears to stall near early adolescence, with little consistency in reported changes during adolescence (Eisenberg et al., 2015). The lack of continued increase in prosocial behavior during this time is puzzling because social-cognitive abilities traditionally theorized to underlie prosocial behavior—such as perspective taking—continue to develop during the adolescent years (Eisenberg et al., 1995, 2005).

Integrating additional theoretical perspectives with traditional theories that emphasize social cognitive developments could help to clarify this puzzling trend. First, rather than simply promoting more prosocial behavior, the social-cognitive and associated brain developments during adolescence may make adolescents more attuned to situational features, such as the recipient of prosocial behavior (Crone & Dahl, 2012). Second, integrated perspectives highlight the relevance of dyadic and group processes, suggesting that prosocial behavior would be higher when potential givers and recipients share relationships and group membership (e.g., friends, family) (Keltner et al., 2014). Finally, the "social reorientation" during adolescence that creates increased salience of peers (Nelson et al., 2005; Steinberg, 2008) may bias adolescents to pay particular attention to whether the recipient is a friend. These additional perspectives, therefore, suggest that social-cognitive and brain developments during adolescence would produce greater differentiation in prosocial behavior according to recipient, with increased preference toward peers in particular during adolescence.

The Utility of Reinforcement Learning in Prosocial Behavior Research

One source of the inconsistency of previous research on prosocial behavior may be the use of multiple methods to assess prosocial behavior including self-report, hypothetical

scenarios, personality assessment, and different reporters (Carlo et al., 1992; Côté et al., 2002; Luengo Kanacri et al., 2013; Soto et al., 2011; Taylor et al., 2013). Thus, an additional way to clarify the actual developmental differences in prosocial behavior is to focus on a behavior that can be readily observed and quantified using a well-established and validated paradigm. In the present study, we utilized a reinforcement learning paradigm to help elucidate trends in cognitive developments (e.g., motivation, learning) that support prosocial behavior.

Past work has frequently utilized reinforcement learning paradigms to assess developmental differences and to understand how adolescents learn and update behavior in non-social contexts (Cohen et al., 2010; Hämmerer et al., 2011; Jones et al., 2011, 2014; Van Den Bos et al., 2012). Interestingly, past work has shown that adolescents tend to outperform children and adults on reinforcement learning paradigms (Davidow et al., 2016; Jones et al., 2014), suggesting something unique about the period surrounding adolescent development. It has been suggested that the heightened reward sensitivity that seems to promote maladaptive risky behaviors in adolescence may utilize the same underlying mechanism that appears to promote learning (Casey, 2015; Spear, 2000). However, this past work examining learning in adolescents has not directly compared differences between self-motivated learning and prosocially-motivated learning. The present study aims to address this gap. Given commonalities in the neural mechanisms underlying risky behavior as well as prosocial behaviors, better understanding learning and decision-making is critical in developing and informing novel interventions that may minimize risky behavior while preserving and enhancing prosocial behavior to maximize overall well-being in adolescence.

Neural Correlates of Learning & Prosocial Behavior

Social cognitive neuroscience has highlighted the role of key neural regions and networks

associated with prosocial behavior among adults, and these regions often overlap with regions implicated in coding learning signals.

Ventral striatum

The ventral striatum, a region often linked with the receipt or anticipation of reward, has been associated with various prosocial or giving behaviors in functional magnetic resonance imaging (fMRI) paradigms. Research has shown that the ventral striatum is active during monetary donations to other entities or individuals (Harbaugh et al., 2007; Moll et al., 2006; Schreuders et al., 2018; Telzer et al., 2013), and that increased striatal activity is associated with choosing to donate more often (Moll et al., 2006). Further, prosocial acts beyond monetary giving, such as giving social support to individuals experiencing physical or social pain, have also been shown to recruit striatal regions (Inagaki & Eisenberger, 2012; Van Der Meulen et al., 2016).

In addition to being recruited during prosocial behaviors, the ventral striatum plays an important role in learning (Adcock et al., 2006; Bunzeck et al., 2010; Wimmer & Shohamy, 2012), suggesting a shared neural underpinning between prosocial behavior and learning. Importantly, then, heightened sensitivity of reward-related regions such as the striatum (as is often observed in adolescent samples (Casey et al., 2008)), might suggest age-related developments in both reinforcement learning and prosocial behavior. In line with this idea, learning signals (which occur when one receives feedback that allows updating of current knowledge) are encoded in the mesolimbic dopamine system (Papageorgiou et al., 2016; Schultz et al., 1997), typically resulting in striatal activity in fMRI paradigms (Christakou et al., 2013; Cohen et al., 2010; Hare et al., 2008; O'Doherty et al., 2003; Van Den Bos et al., 2012). Additionally, neural learning signals in the striatum tend to peak during adolescence (Cohen et

al., 2010), lending support to the idea that enhanced learning during adolescence, particularly learning to benefit others, may be driven by heightened reward sensitivity.

Subgenual anterior cingulate cortex

A second region involved in both learning and prosociality is the subgenual anterior cingulate cortex (ACC). First, the subgenual ACC has been associated with empathy (Rameson et al., 2011; Zahn, de Oliveira-Souza, et al., 2009), an important individual difference measure thought to underlie and motivate prosocial behavior and sentiment. Such empathy-related subgenual ACC activity has further been linked to daily helping behavior (Masten, Morelli, et al., 2011), highlighting the importance of such individual difference measures in the study of prosocial behavior.

Of particular interest to the present work, recent research has found that the subgenual ACC may distinctly code prosocial learning signals (e.g., when one receives feedback that allows updating of current knowledge in the context of learning to benefit others), while the striatum may play a role in coding prediction errors more broadly (learning regardless of recipient) (Lockwood et al., 2016). This work also showed that greater subgenual ACC during prosocial learning was associated with trait empathy, further highlighting empathy as an important correlate of prosocial behavior. Although this past work suggests that increased subgenual ACC activity may be associated with positive social and interpersonal outcomes (e.g., increased empathy, increased prosocial behaviors, better prosocial learning), it is important to note that the subgenual ACC activity has also been identified as an important risk factor for depression, particularly in adolescents (Masten, Eisenberger, et al., 2011; Saxena et al., 2003; Yang et al., 2009). For example, adolescents who exhibit greater subgenual ACC activity in response to peer rejection are at a higher risk for developing depression (Masten, Eisenberger, et al., 2011).

Additionally, this region has also been associated with feelings of guilt, distress, or other negative affect (Masten et al., 2009; Ramirez-Mahaluf et al., 2018; Zahn, de Oliveira-Souza, et al., 2009; Zahn, Moll, et al., 2009). Past work has also shown that deep brain stimulation of the subgenual ACC may reduce symptoms for those experiencing treatment-resistant depression (Mayberg et al., 2005).

One possibility regarding the subgenual ACC is that when prosocial learning signals are more robustly coded in this region (e.g., for those high in trait empathy), such robust subgenual ACC learning signals may lead individuals to shift their behavior trial-by-trial to minimize such neural signals. This is in line with past work linking higher trait empathy to higher prosocial learning rates (Lockwood et al., 2016), which indicates that higher empathy individuals are more heavily weighting recent feedback, and more rapidly shifting their choice behaviors based on that feedback.

Hippocampus

The hippocampus has long been implicated in memory, and is thus important to consider when using a paradigm in which individuals are required to hold multiple cue-target associations in mind throughout a task. For example, the hippocampus interacts with the striatum to support reinforcement learning (Adcock et al., 2006; Wimmer & Shohamy, 2012), and appears to code learning signals as well (Davidow et al., 2016; Hare et al., 2008; Ploghaus et al., 2000). Work in adolescents has shown that adolescents outperform adults on reinforcement learning tasks, partially due to heightened hippocampal activity during learning (Davidow et al., 2016). The hippocampus has also been shown to interact with reward-related regions, such as the striatum, to support better learning in adolescents (Davidow et al., 2016). Thus, better memory for reinforcement events (e.g., feedback after a choice) may underlie better reinforcement learning

performance. These findings underscore the potentially adaptive nature of adolescent reward sensitivity, including supporting reinforcement learning generally. The present study will examine memory for reinforcement events (as well as associated hippocampal activity), and examine differences between self and prosocial learning.

Immune Underpinnings of Health Benefits of Prosocial Behavior

The notion that social relationships are linked with positive physical health outcomes is now decades old, yet the underlying mechanisms of this association continue to be explored. One promising candidate for explaining this link is the immune system—as a great deal of work has shown that positive and negative social experiences are able to causally modulate the immune system, particularly inflammation.

Recent animal work, however, suggests that the cytokine interferon-gamma (IFN-γ) may play a major role in social behavior. Although IFN-γ is involved in inflammatory processes, IFN-γ is unique from other cytokines in that it is critical for antiviral immunity (Cantin et al., 1999; Huang et al., 1993; Müller et al., 1994). Given IFN-γ's role in antiviral processes, an up-regulated antiviral response (e.g., high IFN-γ) may facilitate social interactions, as it protects from viral pathogens which may be transmitted in social contexts. In line with this, IFN-γ knockout mice tend to show autistic-related behaviors such as avoidance of conspecifics. Such behaviors are reversed with injection of recombinant IFN-γ (Filiano et al., 2016), suggesting a causal pathway. Thus, reduced antiviral immunity may facilitate social withdrawal behaviors, presumably as a protective mechanism when vulnerability to infection is high. Finally, recent, preliminary work shows that higher levels of IFN-γ are related to increased social contact, as well as increased psychosocial well-being (Leschak et al., under review). For these reasons, IFN-γ is particularly interesting to examine in regard to prosocial learning, and is currently an

unexplored but promising candidate for probing the well-known association between social relationships and physical health.

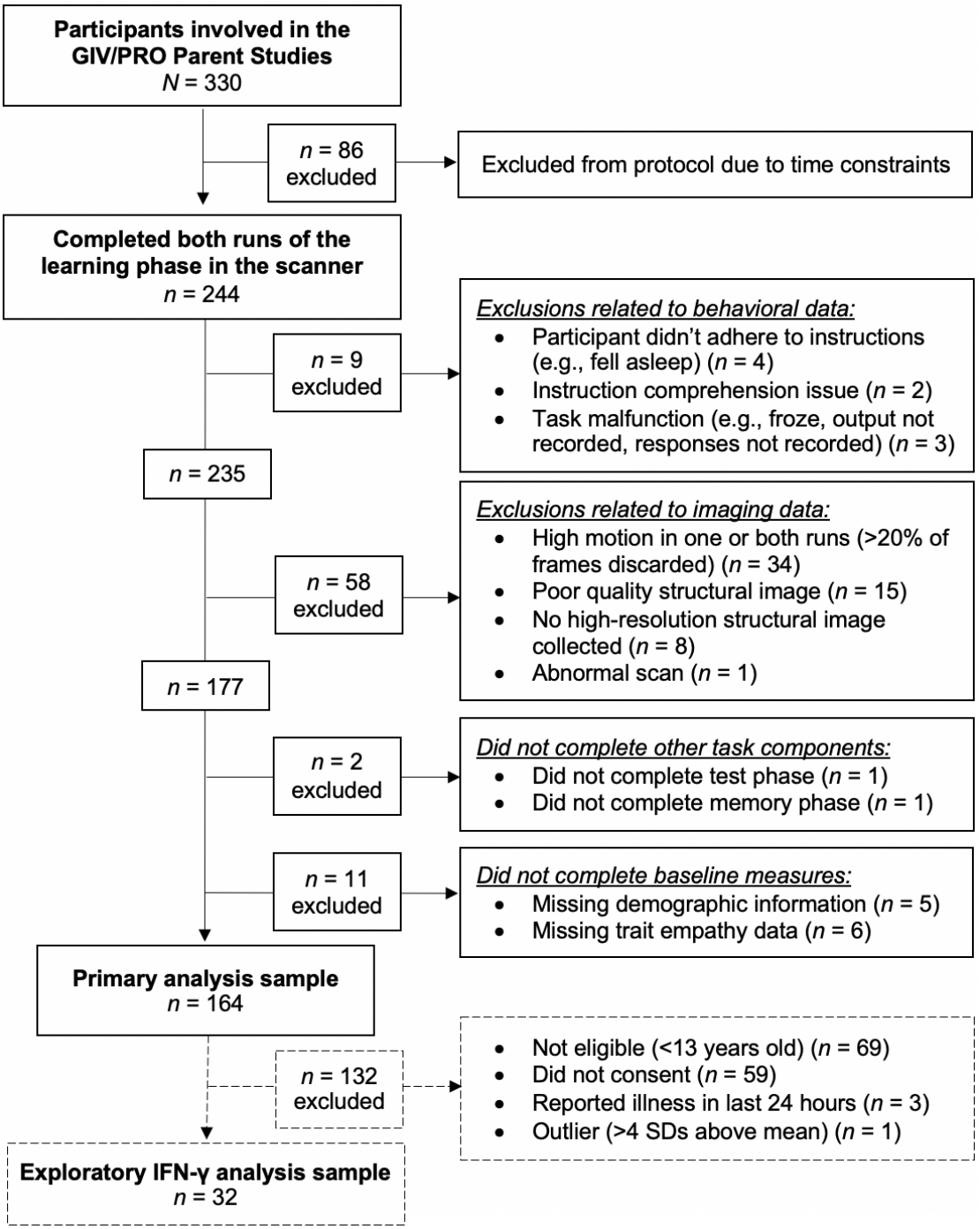
III. Methods

Participants

The final sample utilized in primary analyses consisted of 164 participants aged 9-20 years old (M = 13.68 years, SD = 3.42). See Figure 1 for relevant exclusions. Participants were approximately half female (48.8%).

Figure 1

Flow of Participants through Study and Analysis Pipeline



Note. IFN-γ = interferon-gamma; GIV = cross-sectional parent study; PRO = longitudinal parent study.

Participant Recruitment

Participants were recruited from two ongoing federally-funded studies aimed at understanding the neurodevelopment of prosocial behavior. Half of participants (n = 82; 9-10, 14-15, and 19-20 years old) were recruited from a cross-sectional study ("GIV") funded by the National Science Foundation, while the other half (n = 82; 9-14 years old) were recruited from an ongoing longitudinal study ("PRO") funded by the National Institute of Health. Thus, with the exception of one participant (17 years old)[1], participants were 9-15 years old or 19-20 years old. Study procedures between the two parent studies were identical, with the exception of slight differences in the scanning parameters for the structural brain images (detailed below).

Participants under the age of 18 were recruited via advertising at Los Angeles Unified School District schools, the use of several large databases (University of California Los Angeles [UCLA] Developmental Science Collaboration, Marketing Systems Group GENESYS Sampling Systems), posting advertisements on and near the UCLA campus, and word-of-mouth or referrals from past participants. Young adults (19-20 years old) were primarily recruited from the UCLA undergraduate population, via advertising within UCLA courses and on the broader UCLA campus. Data was collected between May 2017 and January 2020.

Inclusion criteria

To participate in the study, participants were required to meet the following criteria: (i) be within an age-group investigated in the study (9-15, or 19-20 years of age) at the time of the study session; (ii) fluent in English; (iii) not previously diagnosed with a psychiatric disorder;

[1] Due to errors in screening participants, one PRO participant aged 17 participated, despite being outside of the age criteria. In addition, one GIV participant aged 13 participated, despite being outside of the age criteria for that parent study.

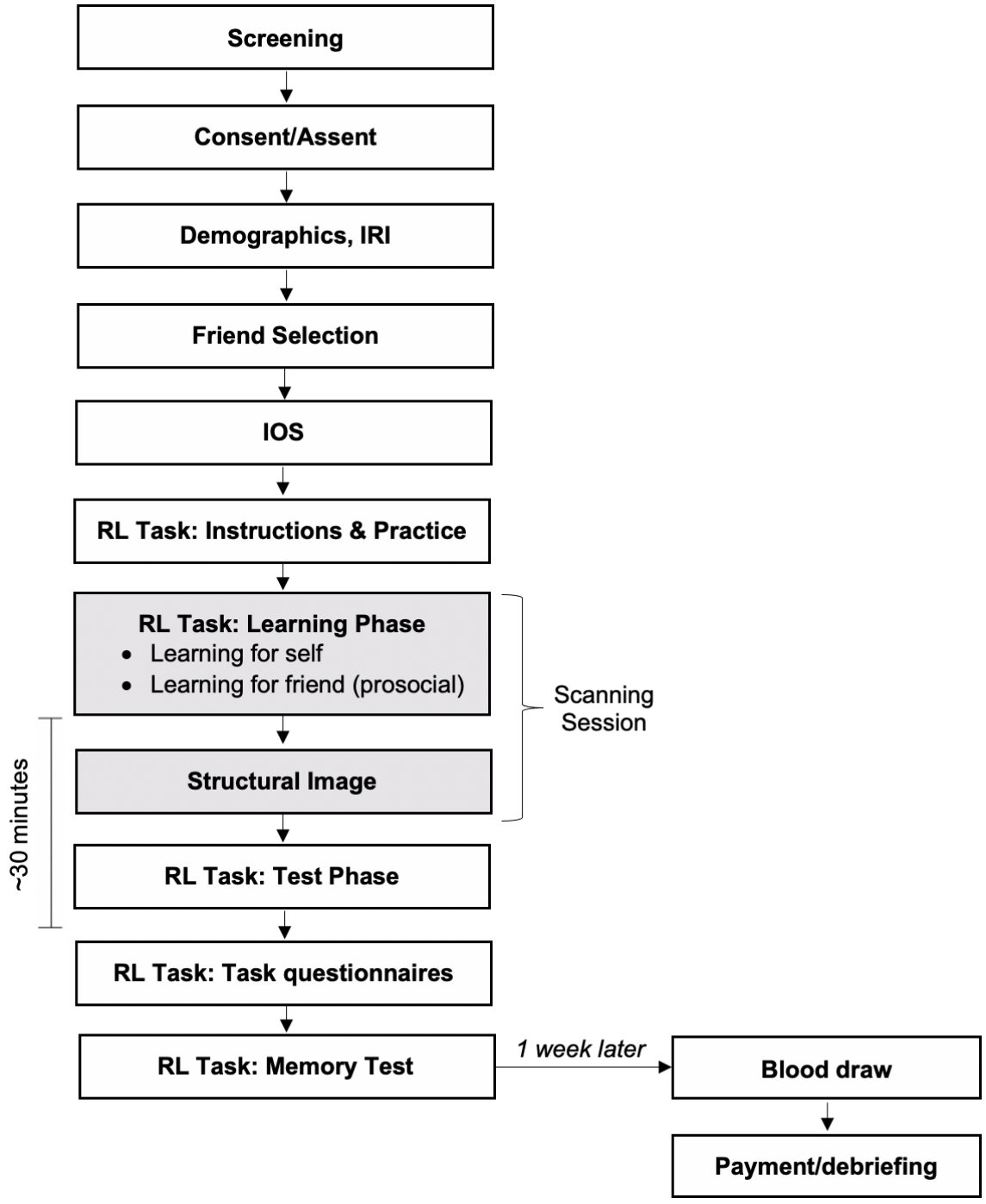
and, due to contraindications for the magnetic resonance imaging session, participants were required to (iv) be right-handed; (v) have no metal in the body (including braces); and (vi) could not be pregnant or trying to become pregnant.

Procedure Overview

After being screened for eligibility, participants completed baseline questionnaires from home, and then came to the UCLA Staglin Center for Cognitive Neuroscience (CCN) for their visit. Consent and/or assent was obtained from all participants. Eligible participants (GIV participants 14 years or older) were asked to participate in an optional blood draw to assess circulating cytokines. Next, all participants selected a close friend of their choosing for whom they played the reinforcement learning task. After completing questionnaire measures about the selected friend, participants then received instructions on the learning phase of the reinforcement learning task, and completed a practice task with follow-up questions probing comprehension of task instructions. They were told the better they do on the learning phase, the more money they would earn for either themselves (self learning) or their selected friend (prosocial learning). They then completed both conditions of the learning phase while undergoing an fMRI scan. Directly after the scan, participants completed the test phase of the reinforcement learning task, and 30 minutes after the scan completed a surprise memory test in order to assess episodic memory of reinforcement events in the learning phase. GIV participants who consented to the optional blood draw re-visited the UCLA campus roughly one week later, where a phlebotomist collected a blood sample via venipuncture. (See Figure 2 for an overview of study procedures.)

Figure 2

Overview of Study Procedures



Note. IRI = Interpersonal Reactivity Index; IOS = Inclusion of Other in Self; RL = reinforcement learning.

Measures

Empathy

Prior to their in-person scanning session, participants completed two subscales of the Interpersonal Reactivity Index (Davis, 1980) in order to assess trait-empathy. The 7-item empathic concern subscale assesses "other-oriented" feelings of sympathy and concern for unfortunate others (e.g., "I often have tender, concerned feelings for people less fortunate than me"). The 7-item perspective taking subscale assesses the tendency to spontaneously adopt the psychological point of view of others (e.g., "I sometimes try to understand my friends better by imagining how things look from their perspective"). All items were answered on a 5-point scale (1 = *does not describe me well*, 5 = *describes me very well*). (See Appendix for full scale.)

Friend Selection and Interpersonal Closeness

Participants were first asked to select a friend, for whom they would later earn money during the prosocial condition of the learning phase (unbeknownst to participants). In selecting this friend, participants were prompted:

> *While you're here, we'll be asking you some questions about a few different people in your life. For example, we'd like you to pick a close friend. This should NOT be a boyfriend, girlfriend, or someone you are related to, but someone you feel really close to and consider a good friend of yours.*

After selecting a friend, participants completed the Inclusion of Other in the Self (IOS) scale (Aron et al., 1992) as a measure of interpersonal closeness with the selected friend.

Reinforcement Learning Task

The reinforcement learning task utilized in the present work is based on traditional,

validated, non-social reinforcement learning paradigms (Foerde & Shohamy, 2011). The task was modified based on previous work examining developmental differences in learning for self (Davidow et al., 2016), and work that has specifically examined reinforcement learning in the context of prosocial behavior (Lockwood et al., 2016). All aspects of the task were presented using PsychoPy (Peirce, 2007).

Instructions and Practice. Next, participants were given instructions for the task and allowed to practice. Participants were told that they would be seeing several different butterflies in the scanner, and each time they saw a butterfly they would also see two different flowers. Each time they saw a butterfly, their job was to try to guess which flower that butterfly was going to land on and feed from in that trial. They were told that each butterfly had a favorite flower that it liked to land on most of the time, and their job was to try to determine the favorite flower of each butterfly through trial and error, and use that information to predict which flower it was likely to land on throughout the task. (See Appendix A for full instruction script.)

In the practice round, participants were presented with 15 trials with a single practice cue (butterfly) and two practice flowers (targets) to become familiar with the task. Just as in the actual learning phase of the task (described below), one of the targets was correct 80% of the time, while the other target was correct 20% of the time. (The actual stimuli presented in the practice task were different than those used in the actual learning task.) After the practice, to be certain that the instructions were correctly understood (particularly for younger participants), experimenters asked follow-up questions probing instruction comprehension. In the event a participant answered any follow-up questions incorrectly, the experimenter reviewed the task with the participant to ensure they had an adequate understanding of the task before continuing.

Learning Phase. Participants completed two runs of the learning phase while undergoing

a functional scan: one run learning cue-target associations to earn money for themselves (self learning), and one run learning to earn money for their selected friend (prosocial learning). In each run, participants saw one of four cues (butterfly) and had to predict which of two targets (flowers) the butterfly was more likely to feed from on each trial. Each cue was associated with one target on 80% of trials and with the other target on 20% of trials. Thus, most of the time, choosing the optimal target for a cue resulted in "correct" reinforcement, but the other 20% of the time resulted in "incorrect" reinforcement, allowing the observation of learning rates over the course of the task as well as the estimation of trial-by-trial expectations and prediction errors.

On each trial, participants had up to three seconds to make a response by pressing a button to choose either the left- or the right-sided target. Participants were encouraged to respond as quickly as possible. If a response was made, their choice was displayed for the remainder of the trial length. After an inter-stimulus fixation (2 s), reinforcement for their choice (e.g., “correct” or “incorrect” feedback) was visually presented on the screen (2 s), along with a an image of a commonplace object or animal. Presentations of these images alongside the feedback allowed us to examine episodic memory for reinforcement events via a surprise memory test (described below). A fixation-cross with a jittered inter-trial interval (2-4 s) followed each reinforcement event.

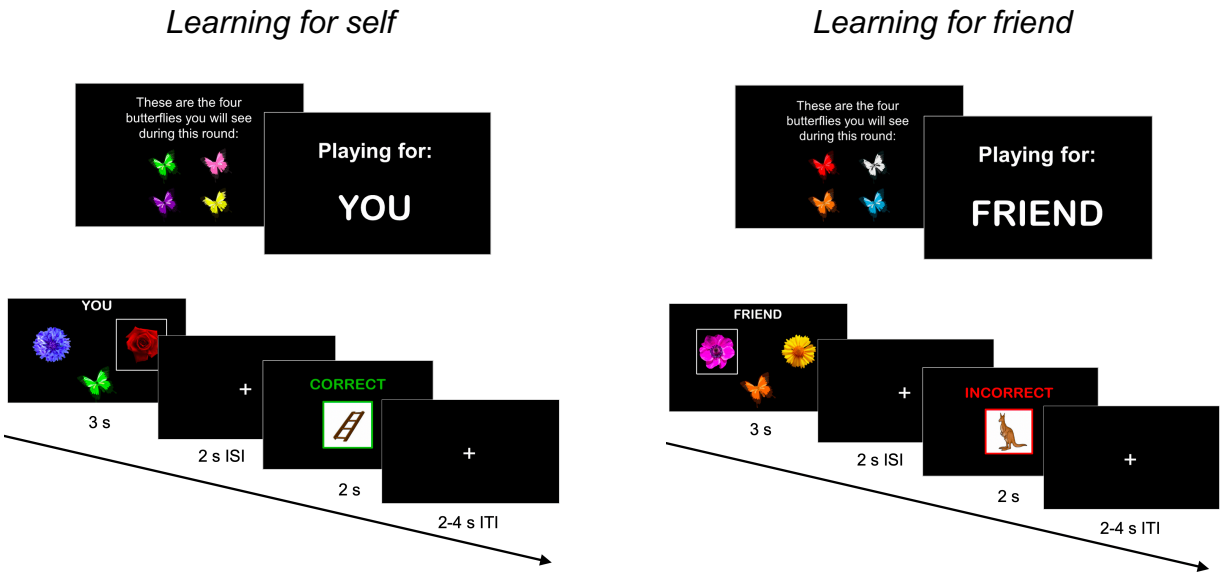
If a participant did not respond in time, no reinforcement was presented, and the words "too late" were presented to preserve timing. These non-response learning trials were discarded from behavioral analysis and modeled as a regressor of non-interest to be kept out of baseline for fMRI analysis (Davidow et al., 2016).[2] Presentation timing of events and jitter durations was optimized for rapid event-related fMRI. Location of targets (left or right) was randomized within

[2] Most participants had very few of these non-response trials, with average response rates of 98.02% and 97.50% in the self and friend conditions, respectively.

each participant. Within participant, the cue and target association were fixed over the entire task. The images presented alongside reinforcement were randomized across participants and conditions, and were orthogonal to the learning task in that they provided no information for learning the cue-target associations. Two fixed cue-target sets (4 cues, 2 targets in each set) were created for the task (see Supplemental Figure 1). Sets were created such that the targets would not match the cues in color. Target order (friend vs. self) was randomized across participants. See Figure 3 for a visual summary of the task design of the learning phase.

Figure 3

Learning Phase Task

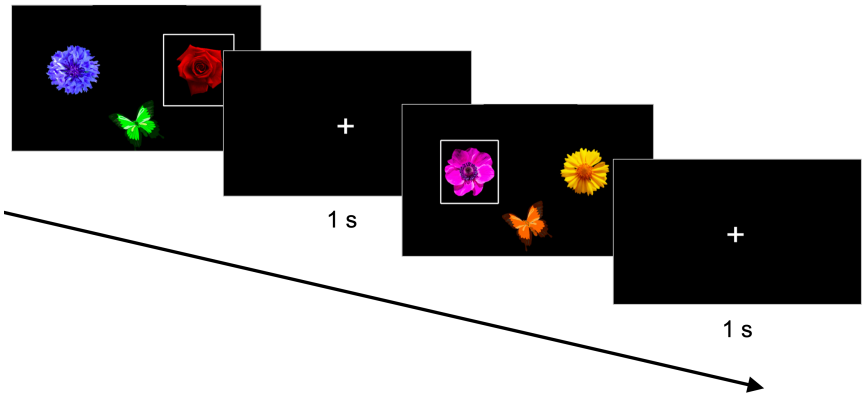


Note. Participants were presented with different butterflies (cues) and tried to guess which flower (targets) a butterfly would feed from on each trial. Following a choice, they were presented with feedback. In the learning for friend condition, the selected friend's first name was displayed for each participant instead of "FRIEND."

Test Phase. Directly after the learning phase, participants completed the test phase of the reinforcement learning task. The test phase was identical in structure to the learning phase, except that it was self-paced, and participants no longer received reinforcement for their choices (and no images were displayed). This provided a measure for how well the associations were learned for each of the cues, in the absence of continued reinforcement. The test phase consisted of 40 trials (each butterfly from the learning phase presented 5 times) in a pseudo-randomized order, such that the same butterfly was never presented twice in a row. (See Appendix B for full instruction script.) See Figure 4 for a visual summary of the task design of the test phase.

Figure 4

Test Phase Task



Note. Participants were presented with the same cues and targets seen during the learning phase, but did not receive reinforcement on their choices.

Post-task Self-Report Measures. After the test phase, participants completed a series of questionnaires that asked about their experience with the learning task.[3] In order to assess the perceived difficulty of learning each butterfly-flower pairing, participants rated how difficult it was to learn the favorite flower for each of the eight butterflies they saw during the learning phase (1 = *easiest to learn*, 8 = *hardest to learn*). In order to assess self-reported effort in each run of the task, participants were asked how hard they tried to get the correct answer in the learning phase for each condition (1 = *not at all*, 7 = *extremely*). In order to assess self-reported attentiveness to the incidental images, we also asked if, while inside the scanner, participants tried to pay attention to the images that were presented alongside feedback (0 = *no*, 1 = *only sometimes*, 2 = *most of the time*, 3 = *yes*).

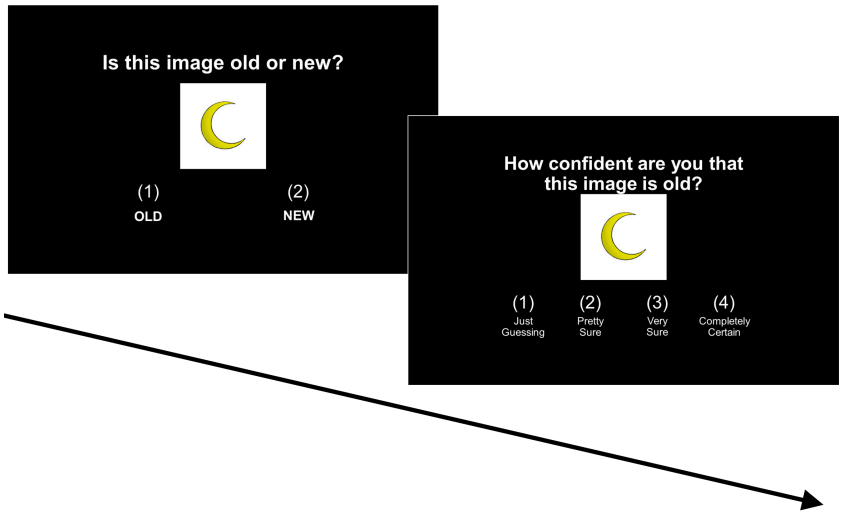
[3] Data for the post-task questions was missing for 1 additional participant.

We also measured how attentive participants were to the incidental images in the scanner by asking them if they tried to pay attention to the objects that were displayed alongside the feedback (0 = *no*, 1 = *only sometimes*, 2 = *most of the time*, 3 = *yes*). This question allowed us to probe whether attentiveness mediated any between-subject differences in memory performance.

Memory Test. About 30 minutes after the learning phase, participants completed a surprise memory test on the incidental images (Figure 5). Participants were shown a total of 120 images (see Appendix D), some of which they had seen presented alongside reinforcement in the learning phase. Participants were asked to indicate whether each image was "old" (shown in the scanner) or "new" (not shown in the scanner), and also indicated how confident they were in each choice (1 = *just guessing*, 4 = *completely certain*). For all subjects, at least 60 of these images were "new" images. The remaining 60 images were those that participants saw during the learning phase (30 from self, 30 from prosocial learning), assuming that they responded to all trials. Since participants were not shown any images for learning trials in which they did not respond, the actual number of "new" vs. "old" images shown to participants varied (e.g., some images that would have been shown during learning were in reality "new" to some participants in the memory test, due to non-response trials). The memory test was self-paced. (See Appendix C for full instruction script.) See Figure 5 for a visual summary of the task design of the memory test.

Figure 5

Memory Test Task



Note. In a surprise memory test, participants viewed images and indicated whether each image was presented alongside reinforcement during learning ("old") or not seen before in the task ("new"). They also provided confidence ratings for their choices.

fMRI Data Acquisition

Imaging data for the learning phase was acquired using a Siemen's Prisma 3.0 Tesla magnetic resonance imaging scanner at the UCLA Staglin CCN. First, we acquired two functional T2-weighted echo-planar image sequences (302 volumes each; slice thickness = 4 mm, repetition time = 2000 ms, echo time = 30 ms, flip angle = 90°, matrix = 64 × 64, field of view = 192). We also acquired a T1-weighted magnetization-prepared rapid-acquisition gradient echo (MPRAGE) anatomical image for functional image registration and normalization (GIV participants: slice thickness = 1 mm, 176 slices, repetition time = 1900 ms, echo time = 2.26 ms, flip angle = 9°, matrix size = 256 × 256, field of view = 250 mm; PRO participants: slice thickness = 1 mm, 192 slices, repetition time = 2000 ms, echo time = 2.52 ms, flip angle = 12°,

matrix = 256 × 256, field of view = 256 mm).

Interferon-gamma (IFN-γ) Assessment

About 1 week after their imaging session, consenting participants (n = 36) provided blood samples were collected by venipuncture into tubes containing ethylenediaminetetraacetic (EDTA) acid. After collection, samples were centrifuged at 4°C, and plasma was harvested into multiple aliquots and stored at -80°C for subsequent batch testing. Once all samples were collected, samples were processed in batch such that all plasma samples from a single subject were assayed together on the same 96-well plate to minimize effects of inter-assay variation. All samples were assayed in duplicate and an internal quality control sample was included on every plate. A multiplex assay utilizing a V-PLEX Custom Human Cytokine Proinflammatory Panel on the Meso Scale Discovery (MSD) electrochemiluminesence platform (Rockville, MD) measured IFN-γ (as well as IL-6, IL-8, IL-10, and TNF-a). Samples were assayed at a 2-fold dilution according to the manufacturer's protocol, with an eight-point standard curve with tripling dilutions. Analyte-specific lower limits were calculated for each assay plate (IFN-γ: .42 pg/mL, IL-6: 0.21 pg/mL, IL-8: 0.17 pg/mL, IL-10: 0.11 pg/mL, TNF-a: 0.11 pg/mL). For all plasma biomarkers, inter-assay coefficients of variation were ≤10% and mean intra-assay coefficients of variation were <6.5%.

Cytokine values were natural log-transformed prior to analyses to correct for non-normality. All analyses involving cytokines also controlled for body mass index (BMI). Participants who indicated being ill in the past 24 hours were excluded from cytokine analyses (n = 3 excluded). One extreme outlier (>4 SDs above the log-transformed mean) was further excluded from IFN-γ analyses. Thus, IFN-γ analyses are based on a subsample of n = 32

participants, ranging in age from 13 to 20 years old (M = 16.63 years, SD = 2.64).

IV. Analytic Strategy

Learning Phase

Because the present task utilized fewer trials than past similar paradigms (Davidow et al., 2016; Lockwood et al., 2016), I first examined whether there was evidence that participants were able to learn across the limited number of trials. To do this, the trials within each run were binned into five blocks consisting of 12 trials per block (similar to prior work, (Davidow et al., 2016)). Thus, each block included 3 presentations of each cue (butterfly). For each block, the percentage of trials for which the participants chose the optimal target was calculated, considered a measure of learning accuracy within each block. I conducted a time (5 blocks) X condition (self learning, prosocial learning) repeated measures analysis of variance (ANOVA) where the dependent variable was the percentage of trials for which the participants chose the optimal target (e.g., learning accuracy) to examine whether there was evidence of learning across time, and whether this learning trajectory differed by condition.

Test Phase

The test phase allowed examination of how well the favorite flowers were ultimately learned for each of the cues, in the absence of continued reinforcement. Thus, the percentage of time the subject selected the optimal cue during the test phase was considered to be the primary measure of learning accuracy. To examine whether learning accuracy in the test phase differed by condition (self learning, prosocial learning), and whether effects varied across age, I conducted a repeated measures ANOVA with condition as a within-subjects factor, including age as a continuous covariate, with the percentage of time the subject selected the optimal cue in the

test phase (e.g., learning accuracy) as the dependent variable.

Memory Test

To assess memory accuracy, a measure derived from signal detection theory, *d*' (d-prime), was computed. In the present task, the "signal" we were interested in detecting is participants' ability to distinguish "old" items from "new" items. Table 1 shows the four possible outcomes for a single trial in the memory task.

Table 1

Potential Outcomes in the Memory Task

		Subject's Response		
		"OLD" ("I saw this image in the scanner.")	**"NEW"** ("I did not see this image in the scanner.")	
Correct Response	**OLD** (The image was presented in the scanner.)	Hit	Miss	Total # of old images presented in memory task
	NEW (The image was not presented in the scanner.)	False Alarm	Correct Rejection	Total # of new objects presented in memory task

Note. Each trial on the memory test can be classified as a hit, a miss, a false alarm, or a correct rejection.

In order to calculate *d*', we calculate the hit rate and the false alarm rate. The *hit rate* (HR) is the proportion of old images accurately classified as "OLD", or the probability that an old image will be classified as "OLD" by the participant:

$$HR = P(\text{"OLD"}|old) = \frac{\#\ of\ hits}{total\ \#\ of\ old\ images}$$

The *false alarm rate* (FA) is the proportion of new images mistakenly classified as "OLD", or the probability that a new image will be classified as "OLD."

$$FA = P(\text{"OLD"}|new) = \frac{\#\ of\ false\ alarms}{total\ \#\ of\ new\ images}$$

In calculating *d*', the HR and FA are z-transformed, and the FA rate is subtracted from the HR:

$$d' = z(HR) - z(FA)$$

Thus, *d*' serves as a sensitivity index, or a measure of the degree to which participants can truly discriminate between old and new images. Unlike using the HR alone as a measure of memory accuracy, *d*' is unaffected by response bias because it takes into account the subject's FA. (A HR of 100% could be achieved by classifying all images in the memory task as "OLD," but would not accurately reflect a subject's ability to distinguish between old and new images, as their FA would also be 100%.)

Because the computation of d' requires the conversion to hit rates and false alarm rates to z-scores, perfect scores (e.g., HR of 100%, FA of 0%) require slight adjustments in order to calculate d'. (Otherwise, the z-score computation would return infinity.) For such scores, the Macmillan & Creelman (1991) adjustment was implemented. This criteria adjusts HR or FA of 1 down to $(1 - 1/(2n))$ and adjusts HR or FA of 0 up to $(1/(2n)$, where n is the number of total

trials for that particular rate. With these adjustments, the effective range of possible d' would be ±4.79 (although values do not typically exceed ±2). Higher scores indicate better accuracy, suggesting the HR is greater than the FA. Negative values would indicate a higher FA than HR (e.g., often misclassifying new objects as old while failing to identify old objects as old), while a d' score of 0 would represent equal HR and FA (e.g., chance performance). Note that various combinations of HR and FA can lead to the same d'.

In the present task, the old images were presented in one of four contexts: 1) alongside positive feedback in the self learning condition alongside positive feedback in the prosocial learning condition, 3) alongside negative feedback in the self learning condition, 4) alongside negative feedback in the prosocial learning condition. Thus, we calculate a separate HR for each of these conditions:

$$HR_{self+} = P(\text{"OLD"}|old_{self+}) = \frac{\#\ of\ hits_{self+}}{total\ \#\ of\ old\ images}$$

$$HR_{self-} = P(\text{"OLD"}|old_{self-}) = \frac{\#\ of\ hits_{self-}}{total\ \#\ of\ old\ images}$$

$$HR_{prosocial+} = P(\text{"OLD"}|old_{prosocial+}) = \frac{\#\ of\ hits_{prosocial+}}{total\ \#\ of\ old\ images}$$

$$HR_{prosocial-} = P(\text{"OLD"}|old_{prosocial-}) = \frac{\#\ of\ hits_{prosocial-}}{total\ \#\ of\ old\ images}$$

Note that the FA remains constant across these conditions, as its computation relies on new images, which are not associated with different conditions. We accordingly calculate separate measures of memory accuracy (*d*') for each condition:

$$d'_{self+} = z\left(HR_{self+}\right) - z(FA)$$

$$d'_{self-} = z\left(HR_{self-}\right) - z(FA)$$

$$d'_{prosocial+} = z\left(HR_{prosocial+}\right) - z(FA)$$

$$d'_{prosocial-} = z\left(HR_{prosocial-}\right) - z(FA)$$

Past work (Davidow et al., 2016) has calculated d' after excluding any trials where participants indicated they were "just guessing" in their confidence ratings. However, this may introduce a new kind of response bias into results: The tendency for participants to indicate that they were just guessing may differ systematically across variables of interest, such as age. Removing guessing trials may also lead to inflation of d' estimates, given that a d' of 0 is intended to present chance performance. In order to achieve a meaningful zero, the inclusion of guessing trials is critical. In addition, in order to calculate the most robust d' for specific 2x2 cells (e.g., d'_{self+},, d'_{self-}, $d'_{prosocial+}$, $d'_{prosocial-}$), utilizing the maximum number of trials available in each cell to calculate the corresponding HR would be ideal. Thus, primary analyses included "just guessing" trials in d' estimates. See Supplement Results for additional analyses regarding the inclusion of "just guessing" trials in computations.

In analyzing performance on the memory test, the aim is to investigate whether participants' ability to accurately recall "old" images (i.e., those presented during learning) differed based on 1) condition (self learning, prosocial learning) and 2) the feedback it was presented alongside (positive feedback ["CORRECT"], negative feedback ["INCORRECT"]).

In order to compare memory accuracy across the conditions, a repeated measures GLM with feedback (positive, negative) and condition (self, prosocial) as within-subject factors was conducted. In order to investigate whether memory accuracy differed by age across these

conditions, age was included as a continuous covariate.

Following prior work which has demonstrated an overall positivity bias in memory (e.g., participants tend to have better memory for objects presented alongside positive feedback), an index of valence bias in memory was computed by taking the difference score for each participant between their memory accuracy for images paired with positive vs. negative feedback ($d'_+ - d'_-$). Thus, positive scores reflect a bias toward remembering images paired with positive feedback, and negative scores reflect a bias toward remembering images paired with negative feedback, while a difference score of 0 reflects equal memory performance regardless of feedback.

Individual Difference Measures

In order to examine how interpersonal closeness with a friend relates to prosocial learning for that friend, Pearson correlations were computed to examine whether overall learning accuracy (in the test phase) during prosocial learning is positively associated with interpersonal closeness.

In order to examine how trait empathy relates to prosocial learning, Pearson correlations were computed to examine whether overall learning accuracy (in the test phase) during prosocial learning is associated with a) empathic concern and b) perspective taking.

Finally, to examine how levels of IFN-γ are associated with prosocial learning, partial correlations (controlling for BMI) were computed to examine whether overall learning accuracy (in the test phase) during prosocial learning is associated with IFN-γ.

fMRI Data Preprocessing

The imaging data were analyzed using Statistical Parametric Mapping (SPM12, Wellcome Department of Imaging Neuroscience, London), and preprocessed through the pipeline outlined below.

Image Quality Inspection

Prior to preprocessing, several quality control measures were conducted to evaluate the validity of each participant's data, and evaluate whether and how it should be included in analyses.

Images were inspected for artifacts, such as aliasing (wraparound), ringing, ghosts, distortion, and dropout. Subjects who were found to have poor quality structural images (e.g., ringing or blurring due to excessive motion) were excluded due to concerns with co-registering functional images to the structural image (n = 15 excluded). One additional participant was excluded due to a structural brain abnormality.

In cases where motion of more than 1 mm from one image to the next (framewise displacement) was detected in functional runs, individual nuisance regressors were added to remove such images from analyses. Subjects who had <80% of their functional volumes remaining in either run after nuisance regressors were removed from subsequent analyses (n = 34 excluded).

Preprocessing

For each subject, functional images were realigned to the mean functional image and resliced to correct for head motion. Additionally, this realignment procedure produced six regressors corresponding to the rigid-body transformations (three rotations and three

transformations). Structural MPRAGE images were then segmented and bias-corrected. Deformation fields were computed for normalizing the MPRAGE to MNI space. Functional images were co-registered to the bias-corrected structural grey matter. All images were then affine registered into Montreal Neurological Institute (MNI) space. The previously generated deformation fields were then used to normalize all images into MNI space, with functional images undergoing integrated spatial smoothing (5 mm, Gaussian kernel, full width at half maximum).

fMRI Data Analysis

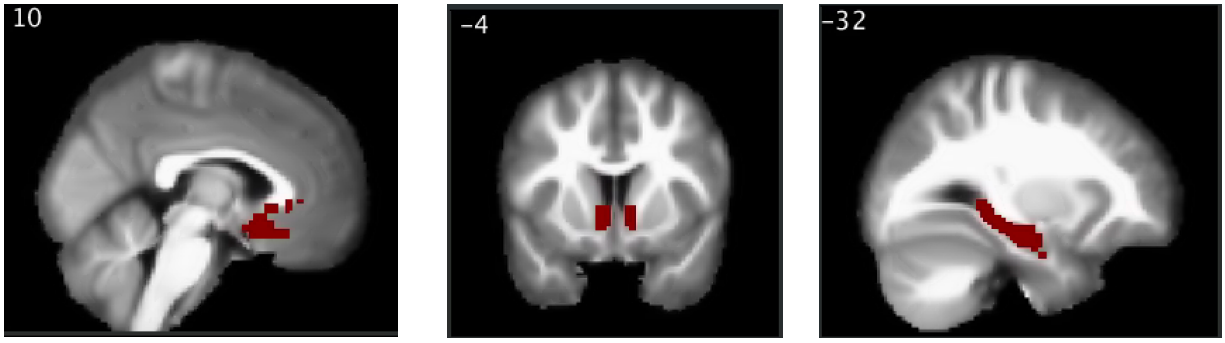
Region of Interest (ROI) Analysis

Parameter estimates were then extracted from the above main effect model for a priori anatomical region of interest (hippocampus, subgenual ACC, striatum), shown in Figure 6.

The hippocampus was defined anatomically using the Automated Anatomical Labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). The subgenual ACC ROI consisted of Brodmann's area 25 and the superior portion ($z < 0$) of Brodmann's area 24 (Lockwood et al., 2016). The ventral striatum ROI was comprised of the left/right caudate and left/right putamen (as defined by the AAL), and then bounded at $-10 < x < +10$, $+4 < y < +18$, $-12 < z < 0$ based on coordinates showing increased VS activity to the anticipation of reward (Knutson et al., 2003, 2007).

Figure 6

Regions of Interest



Note. ACC = anterior cingulate cortex.

Parameter estimates were extracted for $feedback_{prosocial}$ vs. baseline and $feedback_{self}$ vs. baseline contrasts. In order to test whether the neural regions associated with prosocial and self learning differ as a function of age, a repeated measures GLM, with age as a continuous covariate and condition as a within-subjects factor (prosocial, self) was conducted for each of the ROIs. Post-hoc examinations compared the two conditions within each age group, and compared each condition across the age groups.

V. Results

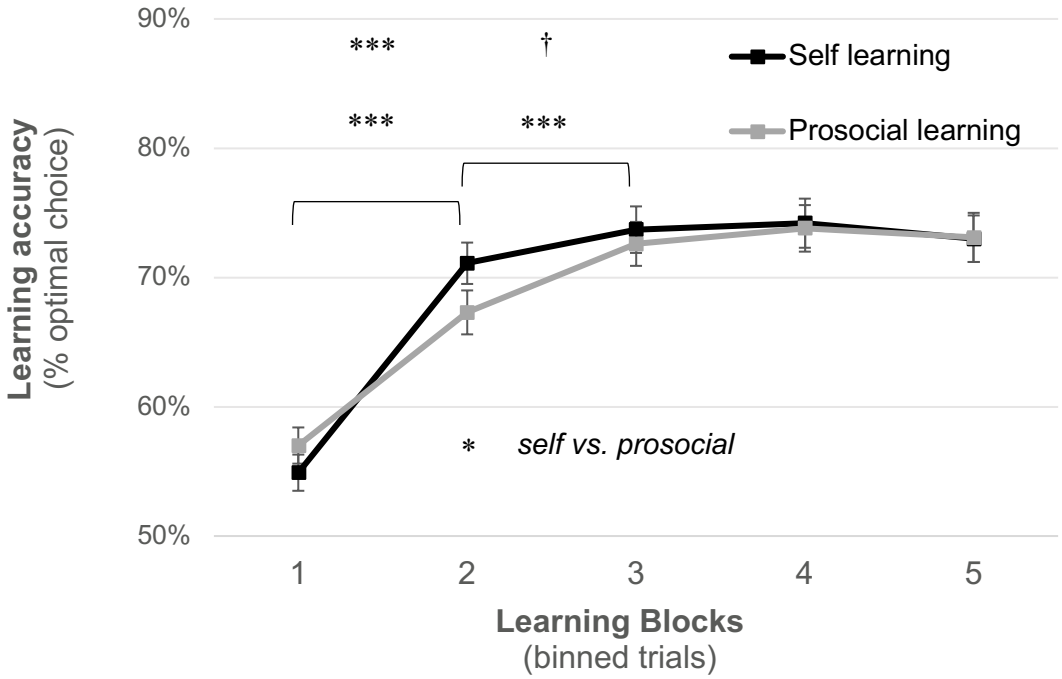
Incremental Learning (Learning Phase)

There was a marginal time X condition interaction, $F(3.38, 551) = 2.241$, $p = .075$ (Greenhouse-Geisser corrected), partial $\eta^2 = .014$ (Figure 7). One-sample t-tests revealed that in both conditions, participants were selecting the optimal target above chance-levels (50%) within the first block after seeing each butterfly only 3 times (self learning: $t(163) = 38.71$, $p < .001$; prosocial learning: $t(163) = 39.80$, $p < .001$). There were no differences between the conditions

in block 1 accuracy, $t(163) = -1.08$, $p = .283$. Further pairwise comparisons showed that in both conditions, participants significantly improved from block 1 to block 2 (self learning: $t(163) = -11.05$, $p < .001$; prosocial learning: $t(163) = -6.31$, $p < .001$). Although there were improvements in both conditions, accuracy in block 2 was significantly higher for self-learning relative to prosocial learning, $t(163) = 2.06$, $p = .041$. From block 2 to block 3, there were significant improvements in prosocial learning ($t(163) = -3.50$, $p < .001$), and marginal improvements in self learning ($t(163) = -1.90$, $p = .059$), such that there were no longer any condition differences. After block 3, performance in both conditions plateaued, with no differences between conditions in block 4, block 5, or block 6 (ps > .475). In short, participants in both conditions demonstrated incremental improvements in learning, although their trajectories differed slightly.

Figure 7

Learning Accuracy Across Time



Note. There was a marginal condition X time interaction (p = .075) such that learning accuracy improved over the course of the task, with accuracy plateauing earlier for self learning while prosocial learning improved more incrementally). Estimated marginal means are plotted with standard error of the means.

***p < .001, **p < .01, *p < .05, $^{\dagger}p$ < .10

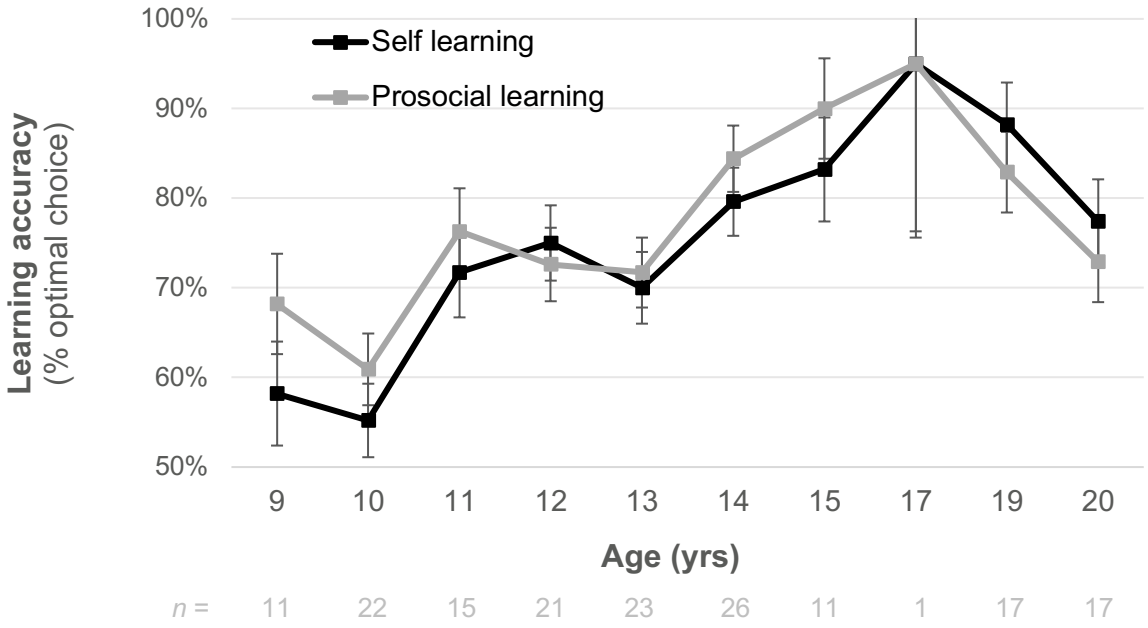
Results using unbinned (trial-level) data resulted in comparable findings (Supplemental Results).

Final Learned Associations (Test Phase)

There was a significant interaction between age and condition (F(1,162) = 4.77, p = .03, partial η^2 = .029) (see Figure 8).

Figure 8

Learning Accuracy Across Age



Note. There was a significant interaction between age and condition (p = .03). The sample size for each age is listed below the x-axis.

To further explore the nature of this interaction effect, we collapsed age into categories in order to have fewer comparisons with greater statistical power. Based on similar levels of learning performance, we collapsed age into the following categories: 9-10 year olds (children; n = 33), 11-13 year olds (early adolescents; n = 59), 14-15 year olds (middle adolescents; n = 38[4]), and 19-20 year olds (young adults; n = 34). We conducted a univariate ANOVA within each

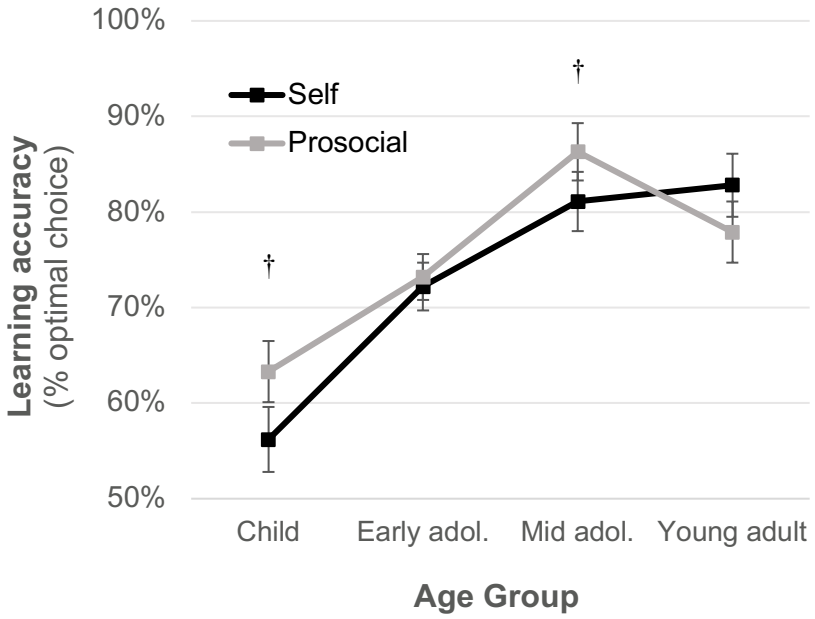
[4] Because the 17 year old fell between our late adolescent group (14-15 year olds) and our young adult group (19-20 year olds), we examined this participant's pubertal stage (as measured by the Pubertal Development Scale) to determine the most appropriate age category. Based on their pubertal classification as "midpubertal," this subject was included in the 14-15 year old age category. Unless otherwise noted, excluding this participant from analyses did not change any results.

condition with age category as a between-subjects factor.

In the self learning condition, children performed worse than all other age groups (ps ≤ .001; see Figure 9). The mid-adolescents did not perform differently than early adolescents (p = .125) or young adults (p = .981). However, young adults performed marginally better than early adolescents (p = .056). In the prosocial learning condition children performed worse than all other age groups (ps < .074). The mid-adolescents performed better both younger age groups (ps < .005), but their performance did not differ from the young adults (p = .231). Paired t-tests within each age category revealed that children and mid-adolescents performed slightly better in the prosocial condition on the test phase (children: $t(32) = –1.71$, p = .097; mid-adolescents: $t(37) = – 1.741$, p = .090). There were no differences by condition for early adolescents ($t(58) = –0.39$, p = .695) or for young adults ($t(33) = 1.58$, p = .124).

Figure 9

Learning Accuracy Across Age Category by Condition



Note. Children and mid-adolescents performed marginally better in the prosocial condition relative to the self condition (*p*s < .10). Across both conditions, children performed worse than all other age groups (*p*s < .001). In the self learning condition, there was evidence that age-related improvements continued across the age span, while prosocial learning appeared to peak around mid-adolescence. Estimated marginal means and standard errors are plotted.

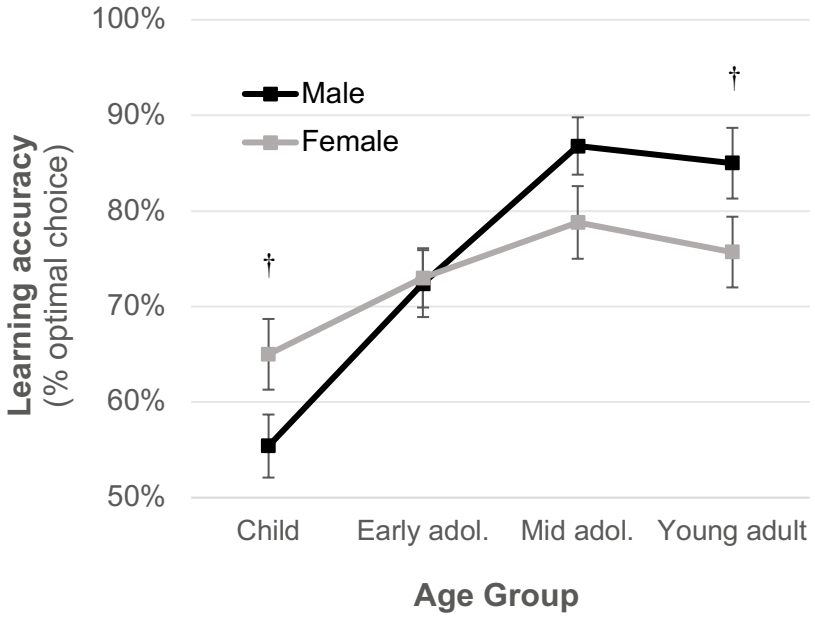
†*p* < .10

As an exploratory analyses, effects of participant sex were examined. There was no significant three-way interaction between sex, age, and condition $F(1,160) = .022$, $p = .883$). However, there was a significant sex by age interaction ($F(1,160) = 5.751$, $p = .018$), in addition to the significant age X condition interaction reported above. Female children marginally outperformed their male counterparts ($p = .063$), while male young adults marginally outperformed their female counterparts ($p = .087$). There was no statistically significant

difference between the performance of males and females in the early adolescent age group (p = .906). Although it did not reach the statistical criteria to be considered marginal, middle adolescents showed a similar trend as young adults, such that males slightly outperformed females (p = .106). (See Figure 10.)

Figure 10

Learning Accuracy Across Age Category



Note. Female children marginally outperformed their male counterparts (p = .063), while male young adults marginally outperformed their female counterparts (p = .087). There were no statistically significant differences between the performance of males and females in the adolescent age groups (ps > .106).

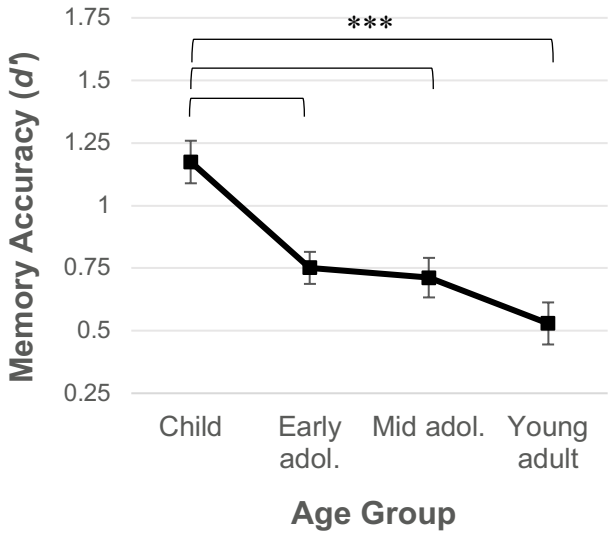
†$p < .10$

Memory Accuracy by Feedback

First, I examined whether episodic memory for reinforcement events (as measured by d') differed by age, condition (seen during self or prosocial learning, seen during prosocial learning), and feedback (seen with positive or negative feedback). In a repeated measures ANOVA with age entered as a continuous covariate, and condition and feedback as within-subjects repeated factors, the only effect that emerged was a significant effect of age on memory accuracy, $F(1,160) = 19.992$, $p < .001$, such that performance decreased across age. There was no significant three-way interaction between age, condition, and feedback ($F(1,160) = 1.908$, $p = .169$), and no significant two-way interactions (feedback X age: $F(1,160) = 1.274$, $p = .261$; condition X age: $F(1,160) = .124$, $p = .725$). There were also no main effects of condition or feedback ($F(1,160) = .018$, $p = .892$, $F(1,160) = .632$, $p = .428$, respectively). Thus, to explore the significant effect of age on memory performance, we conducted a more parsimonious univariate ANOVA in which age group was included as a between subjects factor and overall d' (regardless of condition and feedback) was included as the dependent variable (Figure 11). Pairwise comparisons showed that children had better episodic memory for reinforcement events compared to all other age groups (ps < .001).

Figure 11

Episodic Memory for Reinforcement Events by Age Group



Note. Children outperformed all other age groups in terms of accuracy on the memory task.

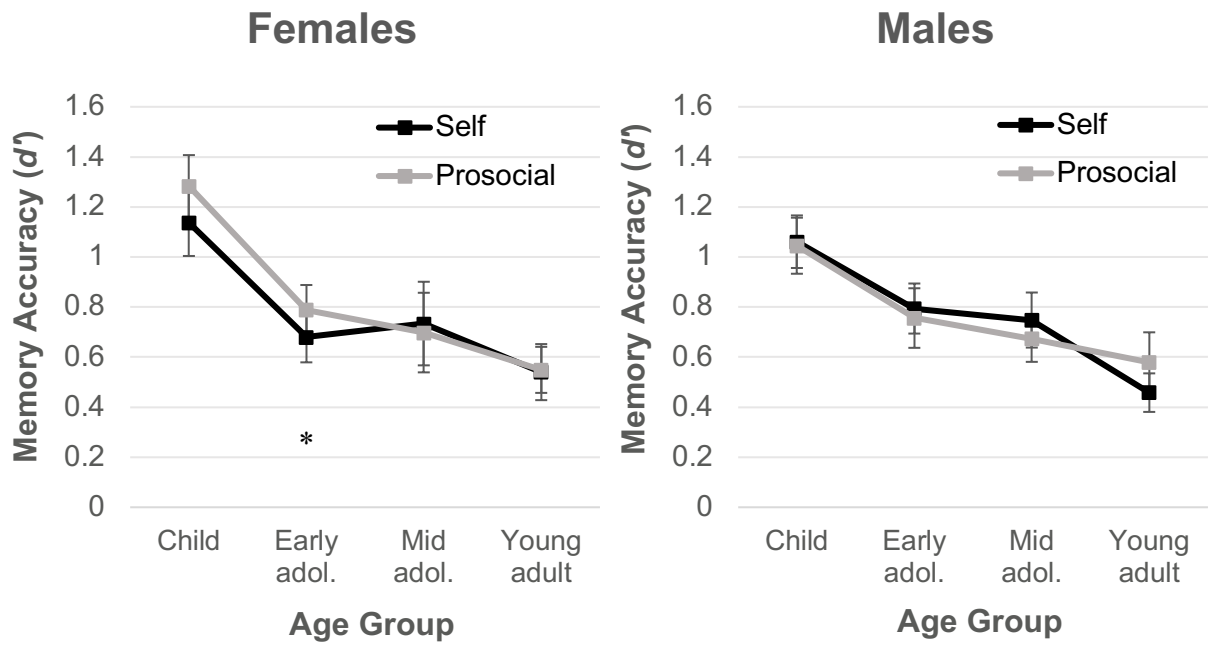
***$p < .001$

As an exploratory analysis, I examined potential effects of participant sex on memory accuracy in a model including condition, feedback, sex, and age. As there was no significant 4-way interaction ($F(1,158) = 1.929$, $p = .167$), as well as no other significant effects or interactions relating to feedback in this model (ps >.169), I conducted a more parsimonious model including only condition, sex, and age. In this model, there was a marginal 3-way interaction, $F(1,159) = 3.583$, $p = .060$ (see Figure 12). For both males and females, there was no significant condition X age interaction (males: $F(1,82) = 1.845$, $p = .178$); females: $F(1,77) = 1.831$, $p = .180$). In addition, there were no significant condition X sex interactions within the age categories (children: $F(1,30) = 1.163$, $p = .289$; early adolescents: $F(1,57) = 2.187$, $p = .145$; mid-adolescents: $F(1,36) = .094$, $p = .760$; young adults: $F(1,32) = .652$, $p = .425$). Simple main effects of condition within each age group and sex only revealed a significant effect of condition

for female early adolescents, such that they had better episodic memory for images presented during prosocial learning, relative to memory for images presented during self learning, $F(1,32) = 4.310$, $p = .046$.

Figure 12

Episodic Memory for Reinforcement Events by Age Group, Sex, and Condition



Note. Early adolescent females had better episodic memory for images presented during prosocial learning, relative to memory for images presented during self learning.

*$p < .05$

Individual Difference Measures

Interpersonal closeness

There was not a significant interaction between interpersonal closeness with the friend and age on prosocial learning accuracy, $F(1, 160) = .121$, $p = .729$. Further, there was no main

effect of interpersonal closeness on prosocial learning accuracy, $F(1,160) = .299$, $p = .585$. An exploratory model including sex also did not reveal any additional effects (all ps > .142).

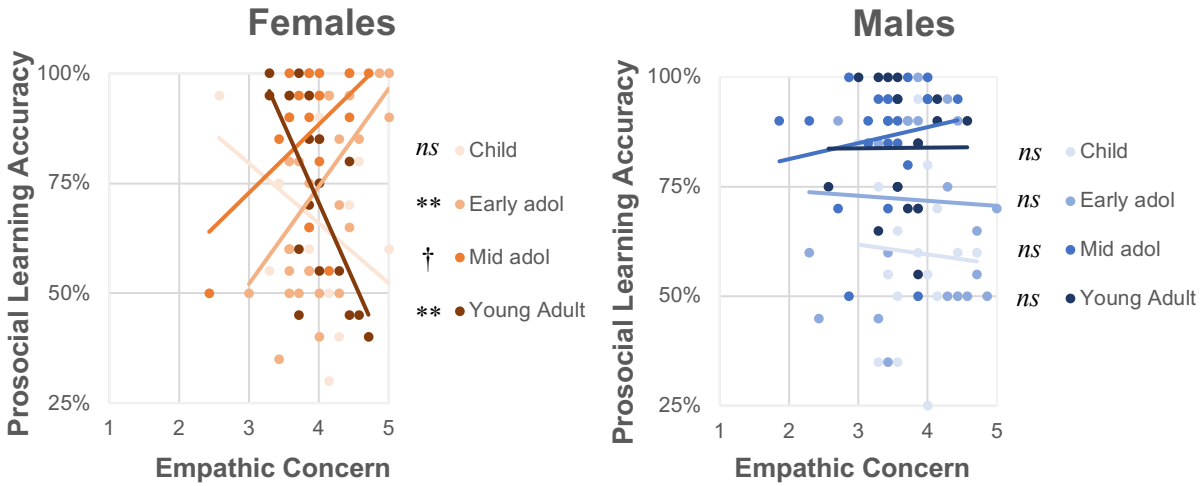
Empathic Concern

There was not a significant interaction between empathic concern and age on prosocial learning accuracy, $F(1, 160) = 2.32$, $p = .130$. Further, there was no main effect of empathic concern on prosocial learning accuracy, $F(1,160) = 1.948$, $p = .165$. However, an exploratory model including sex revealed a marginal three-way interaction between age, participant sex, and empathic concern on prosocial learning accuracy, $F(1, 156) = 2.993$, $p = .086$ (Figure 13). To probe the nature of this interaction, separate univariate ANOVAs were conducted for males and females. While there was no significant interaction between age and empathic concern for male participants ($F(1,80) = .423$, $p = .517$), there was a marginally significant interaction for female participants, $F(1,76) = 3.034$, $p = .086$. Specifically, for female children, empathic concern was not significantly associated with prosocial learning accuracy ($p = .142$). However, for female adolescents, greater empathic concern was associated with higher prosocial earning accuracy (early adolescents $p = .003$; middle adolescents $p = .062$). Interestingly, in young adult females, the direction of this association flipped, such that those with higher empathic concern had lower prosocial learning accuracy ($p = .002$).[5]

[5] Interestingly, this interaction between empathic concern, age, and sex was unique to prosocial learning accuracy. No significant interactions or effects were found when examining effects of empathic concern on self learning accuracy. (See Figure S8.)

Figure 13

Association between Empathic Concern and Prosocial Learning Accuracy Across Age and Sex



Note. There was a marginal interaction between age and empathic concern for females (p = .086), but not males (p = .517).

**p < .01, *p < .05, $^{\dagger}p$ < .10

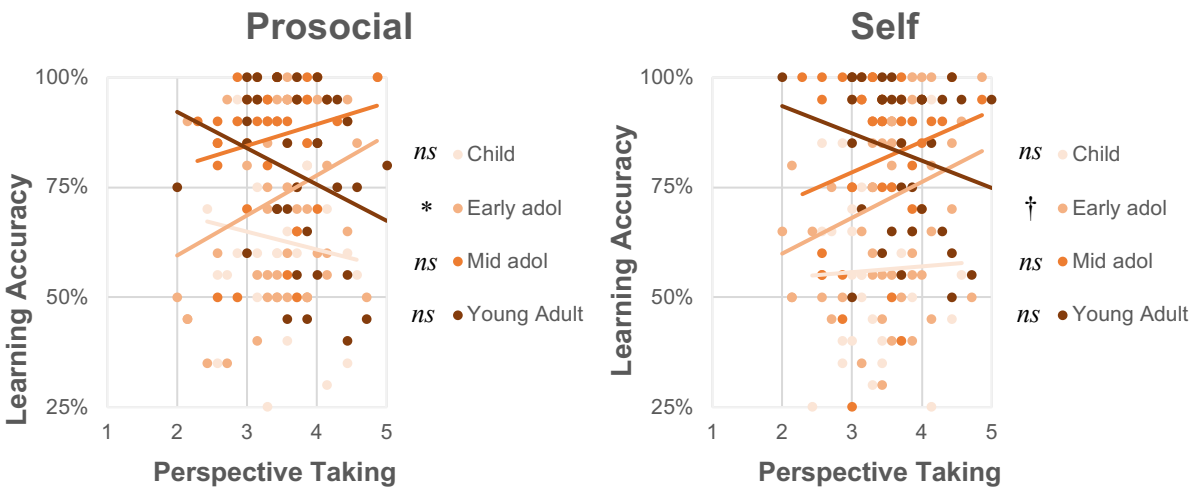
Perspective Taking

There was a marginal interaction between perspective taking and age on prosocial learning accuracy, $F(1, 160) = 3.846$, $p = .052$.[6] There was a significant, positive association between perspective taking and prosocial learning accuracy for early adolescents only (p = .034). However, this age group also showed a similar association between perspective taking and self learning accuracy (p = .058). (See Figure 14.)

[6] An exploratory model including sex did not reveal any effects pertaining to participant sex and perspective taking on learning accuracy. See Figures S9 and S10.

Figure 14

Association between Perspective Taking and Prosocial Learning Accuracy Across Age



Note. There was a marginal interaction between perspective taking and age on prosocial learning accuracy ($p = .052$). However, there was also a significant interaction between perspective taking and age on self learning accuracy ($p = .037$).

*$p < .05$, †$p < .10$

IFN-γ

Finally, circulating levels of IFN-γ were not significantly associated with prosocial learning (controlling for BMI), $r = .207$, $p = .234$. Levels of IFN-γ were also not significantly associated with trait perspective taking ($r = .145$, $p = .436$) or trait empathic concern ($r = .016$, $p = .932$). See Table S2 for associations with other cytokines.

Neuroimaging Results

Subgenual anterior cingulate (subACC)

For subACC activity during the feedback portion of trials (e.g., learning), there was no

condition (self, prosocial) X age interaction, $F(1, 162) = 2.163$, $p = .143$. In addition, there was no main effect of condition on subACC activity, $F(1, 162) = 2.261$, $p = .135$. Finally, there was no main effect of age on subACC activity during learning, $F(1, 162) = .820$, $p = .366$.

Ventral striatum (VS)

For VS activity during the feedback portion of trials (e.g., learning), there was no condition (self, prosocial) X age interaction, $F(1, 161) = .149$, $p = .700$. In addition, there was no main effect of condition on VS activity, $F(1, 161) = .256$, $p = .613$. Finally, there was no main effect of age on VS activity during learning, $F(1, 161) = .110$, $p = .740$.

Hippocampus

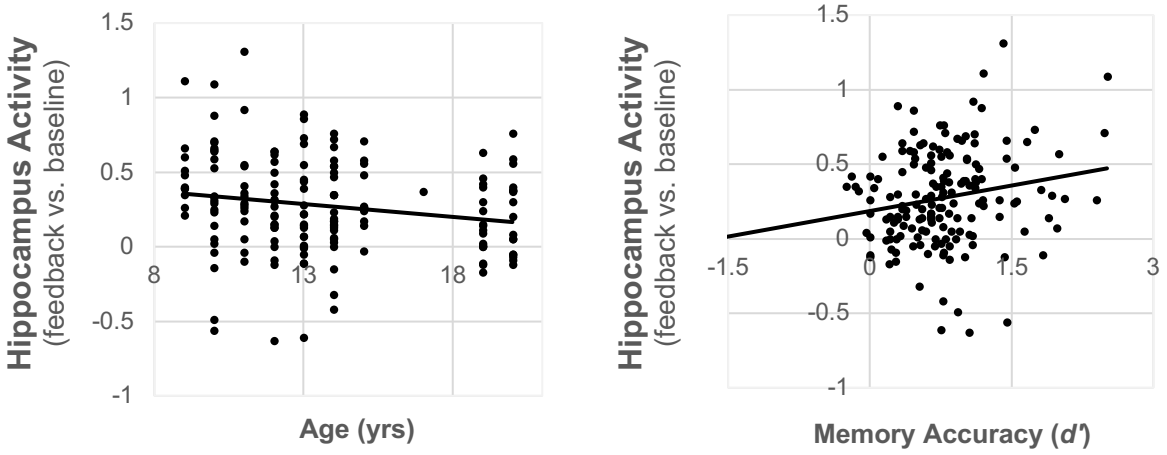
For hippocampus activity during the feedback portion of trials (e.g., learning), there was no condition (self, prosocial) X age interaction, $F(1, 161) = .028$, $p = .867$. In addition, there was no main effect of condition on hippocampus activity, $F(1, 161) = .030$, $p = .863$. However, there was a significant main effect of age on hippocampus activity during learning, $F(1, 161) = .5.812$, $p = .017$. Younger participants tended to show greater hippocampus activity during learning.

Given that analysis of the memory test revealed age-related differences in memory performance (ability to recognize previously seen images), associations between hippocampus activity and memory performance were explored. Hippocampus activity during learning was significantly associated with memory accuracy (d-prime; see Figure 15), such that participants who displayed greater hippocampus activity during learning (feedback vs. baseline) performed with higher accuracy on the memory test, $r = .189$, $p = .015$.[7]

[7] The reported association between age and memory accuracy (d-prime) remained significant ($p < .001$) after controlling for hippocampus activity during learning.

Figure 15

Association between Hippocampus Activity during Learning and Memory Accuracy



Note. There was a main effect of age on hippocampus activity during learning, such that younger participants had higher hippocampus activity (left, $p = .017$). Hippocampus activity was also positively correlated with memory accuracy (right, $p = .015$).

VI. Discussion

In the present study, we found that participants were able to learn cue-target associations within 9 repeated trials for a single cue. After this time, additional trials did not significantly enhance participants' ability to learn and select the optimal target. Although having so few trials precludes the computation of reliable parameter estimates (e.g., learning rates, prediction errors) within traditional reinforcement learning models, abbreviated learning paradigms may be utilized in behavioral research. Given that learning rates are typically inversely associated with performance (e.g., learning accuracy) (Davidow et al., 2016), accuracy may be used as a proxy for such measures that cannot be reliably computed in such limited trial learning tasks. In particular, abbreviated paradigms would be advantageous for assessing learning in younger

samples or other populations that may not be able or willing to endure longer tasks or the constraints of lengthy MRI scans (e.g., ADHD).

The observed trajectory of learning across the binned blocks in the learning phase was remarkably similar between self and prosocial learning. The only significant difference between the conditions was observed in the early phase of learning (block 2), where differences between conditions appeared driven by a steeper learning trajectory for self learning, and a more gradual trajectory for prosocial learning. In addition, there were no observed differences in neural responses to self vs. prosocial learning. The similarity in findings for self and prosocial learning may be a result of the lack of salience of the manipulation during the learning phase. The conditions only differed in terms of who monetary outcomes were directed towards (e.g., earning money for self vs. earning money for friend). This manipulation may have been unsuccessful, particularly because participants were responsible for distributing the resulting monetary rewards to the selected friend. Thus, if participants did not intend to distribute the money to the friend and instead planned to keep the money for themselves, it would not be surprising to see null findings between the self and prosocial conditions. Future work should ensure that similar manipulations are made especially salient and consequential for participants. In other words, future paradigms should include explicit follow-up with participants in order to assess if they indeed provided the friend's earnings to the friend, so that further analysis could split data based on this behavior. Alternatively, a paradigm might instead involve the experimenter taking the burden of distributing the monetary reward, to ensure the recipient of the monetary outcome is consistent across participants (rather than relying on the participants' post-study behavior to ensure this).

In the present study, when examining overall accuracy of learned cue-target associations,

children performed worse than all other age groups. In the self learning condition, there was evidence that age-related improvements in accuracy continued across the measured age span, while prosocial learning appeared to peak around mid-adolescence (14-15 years of age). Although mid-adolescents did not significantly differ from early-adolescents or young adults, this trend is in line with evidence suggesting that, due to a convergence of developmental changes (e.g., increased socio-cognitive abilities, increased sensitivity to peer-relevant information), adolescents may be well-suited to quickly learn new information that is critical for acting prosocially. Prior work that has found differences in learning outcomes between adolescents and adults (Davidow et al., 2016) have focused on later adolescence. Thus, it is possible that significant differences between self and prosocial learning may have emerged had the current sample included participants who were between 16 and 18 years old.

Interestingly, although children underperformed relative to all other age groups in terms of learning accuracy, children outperformed all other age groups in terms of memory accuracy. This inverse pattern may be evidence of some cognitive trade-off between the two processes. However, memory and learning are tightly intertwined and highly dependent processes (Collins & Frank, 2012; Dickerson & Delgado, 2015). Accurate memory of feedback on earlier trials is critical to accurately learning the cue-target associations across the entire task. One possibility is that children paid more attention to the incidental images that were paired along with the feedback, rather than paying attention to the meaning of the feedback itself. This increased attention to the images in children may have occurred because the images were cartoon versions of everyday objects and animals, and thus may have been more appealing and interesting to younger age groups, as compared to if the images had instead been more realistic in nature. This explanation would be in line with past work linking increased salience with memory recall (Fine

& Minnery, 2009). However, there were no differences in the self-reported degree to which participants paid attention to the images, suggesting that such age effects were not driven by conscious effort to attend to the objects. Nonetheless, they may have been easier for younger participants to remember given the age-relevance of cartoon images.

In the present study, self-reported interpersonal closeness with the selected friend was not associated with any outcomes related to prosocial learning. However, within female participants, empathic concern was differentially associated with prosocial learning accuracy across age. Empathic concern was not associated with prosocial learning for children, but was positively associated for both adolescent groups, and negatively associated for young adult females. Although the inverse association between empathy and prosocial learning accuracy observed in young adult females seems counterintuitive, it is consistent with past research showing that young adults who are high in trait empathic concern perform worse on prosocial learning tasks (Lockwood et al., 2016). While mounting evidence has linked empathy with increased overt prosocial behavior (Fraser et al., 2012; Graaff et al., 2017; Masten, Morelli, et al., 2011; Morelli et al., 2014), the current paradigm investigated prosocial learning, a cognitive correlate of prosocial behavior. One potential explanation for this inverse relationship between empathy and prosocial learning performance is that highly empathetic individuals may be more reactive in response to other-relevant feedback. A person high in empathic concern by definition tends to experience other-oriented emotions to a greater degree than someone low in empathic concern (Davis, 1983). Thus, the choice behavior of someone high in empathic concern may be more impacted by feedback in response to a previous choice. As a result, those high in empathic concern may behave in a more volatile manner, heavily weighting recent feedback to update their future choice behavior, rather than taking into account a larger number of past trials. This

more volatile behavior would lead to worse performance (i.e., lower accuracy) (Sutton & Barto, 2017), as was observed here.

Finally, there was no significant ventral striatum or subgenual anterior cingulate activity during learning in the present study. This may have been because the present study examined average activity across all learning trials, whereas past work has found that these regions may be specifically modulated by the degree of prediction errors during learning.[8] Activity in these regions during learning did not differ across condition or age. Although there was no main effect of hippocampus activity during learning, there was a significant main effect of age such that younger participants showed greater hippocampus activity during learning (across both conditions). This increased activity in the hippocampus, a region known to play a role in episodic memory, likely contributed to children's increased memory performance observed in the present study.

The present work found no significant associations between IFN-γ and any measure related to prosociality in the present study. However, several limitations of the current study design should be noted when considering the null effects. First, the blood sample from which measurements of IFN-γ came was taken two weeks after all other study measures. Thus, had our IFN-γ measurement taken place more closely to other measures of interest, such as the prosocial learning paradigm, we may have been more likely to observe significant effects. Additionally, because the blood draw was optional, and only offered to a restricted age range of participants, there was a limited sample available to conduct exploratory analyses relating to IFN-γ.

Future work should continue to explore the utility of reinforcement learning models as a tool to quantify and model such behavior across development. Specifically, future work should

[8] Due to a reduced number of trials used in the present learning paradigm, we were not able to calculate trial-by-trial prediction errors.

focus on paradigms with sufficient trials to compute subject-level parameters such as learning rates across conditions. This would simultaneously enable more reliable trial-level estimates of prediction errors, which was not possible in the present study. Further, such work should aim to examine associations between prosocial acts and markers of physical health that have been observed in adult populations, in an effort to understand their emergence across development. In particular, additional work on IFN-γ in humans and how it may relate to social behavior is needed.

VII. Appendices

Appendix A: Empathic Concern (EC) and Perspective Taking (PT) Measure

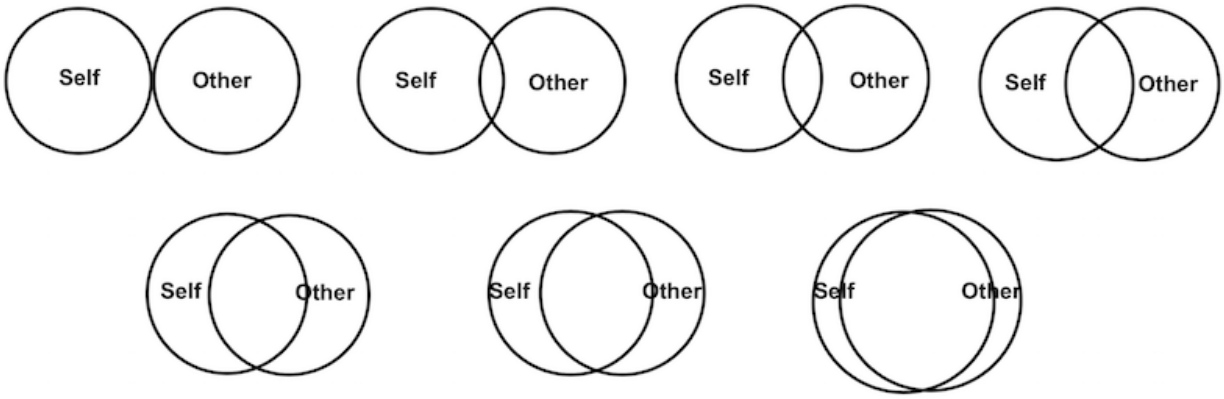
The following statements ask about your thoughts and feelings in a variety of situations. For each statement, indicate how well it describes you. Read each statement carefully. Answer as honestly as you can.

0	1	2	3	4
Does not describe me at all	Does not describe me	Describes me somewhat	Describes me well	Describes me very well

1. I often have tender, concerned feelings for people less fortunate than me. (EC+)
2. I sometimes find it difficult to see things from the "other person's" point of view. (PT-)
3. Sometimes I don't feel very sorry for other people when they are having problems. (EC-)
4. I try to look at everybody's side of an argument before I make a decision. (PT+)
5. When I see someone being taken advantage of, I feel kind of protective towards them. (EC+)
6. I sometimes try to understand my friends better by imagining how things look from their point of view. (PT+)
7. Other people's troubles do not usually disturb me a great deal. (EC-)
8. If I'm sure I'm right about something, I don't waste much time listening to other people's arguments. (PT-)
9. When I see someone being treated unfairly, I sometimes don't feel very much pity for them. (EC-)
10. I am often quite touched by things that I see happen. (EC+)
11. I believe that there are two sides to every question and try to look at them both. (PT+)
12. I would describe myself as a pretty soft-hearted and sensitive person. (EC+)
13. When I'm upset at someone, I usually try to "put myself in their shoes" for a while. (PT+)
14. Before criticizing somebody, I try to imagine how I would feel if I were in their place. (PT+)

Appendix B: Inclusion of Other in the Self Scale

Please select the picture that best describes your relationship with your friend, ___[NAME]___.



Appendix C: Instructions for the Learning Phase of the Reinforcement Learning Task

"In this game, you will see different butterflies and flowers. You have one main goal: Figure out each butterfly's favorite flower. Throughout the game, you will guess where each butterfly will feed from. To select the flower on the left, press the first button. To select the flower on the right, press the second button. After you've chosen a flower, you will be shown whether or not you guessed correctly. It will also show a picture. If you chose correctly, the screen will say CORRECT in green, and the picture will have a green border. If you chose incorrectly, the screen will say INCORRECT in red, and the picture will have a red border. If you did not choose a flower before the 3 seconds were up, the screen will say OUT OF TIME in red, and will not show a picture.

Each butterfly has a favorite flower which it likes to feed from most of the time, but, occasionally, it will also feed from the other flower. Over time, the answers you get about whether you chose correctly will help you figure out each butterfly's favorite flower. Once you figure out a butterfly's favorite flower, you can use that information to help you guess where it will feed from. It makes sense to always guess that a butterfly will feed from its favorite flower.

You will play two rounds of the game. Each round, you will be playing for a different person. In one round, you will be playing for yourself. In this round, the better you do on the task, the more money you can win for yourself. In another round, you will be playing for your friend. In this round, the better you do on the task, the more money you can win for your friend. Each round, the computer will tell you who you'll be playing for. There will also be a reminder at the top of the screen throughout the game. You'll have 3 seconds to choose one of the flowers. Try to choose a flower every time a butterfly is on the screen.

The side of the screen that the flowers appear on (left vs. right) does not matter. It also does not matter when you see the flowers and butterflies during the task. The favorite flower of each butterfly will stay the same throughout the entire task. In just a minute, you will practice so you know what to expect in the scanner. The butterflies and flowers you see right now in the practice are different from the ones you will see in the scanner. Your score on the practice won't count towards your score in the real game. For the practice run, we'll have you play for yourself. Do you have any questions about the Butterfly Game?"

[*Participant completes practice trials*]

"Did you figure out which flower was the rainbow butterfly's favorite?"

> [*Participants respond by selecting one of the following: (1) Yes! I'm sure which flower was the favorite. (2) I think I might know, but am not really sure. (3) I have no idea which flower was the favorite. For participants who answered (3), experimenters went over the instructions again to ensure participants understood the task, and allowed participants to complete the practice again if they wished. Participants answering (1) or (2) were asked the next question.*]

"Which flower was the favorite? [*participant responds*] Great job! [*if correct*]/ Uh oh! [*if incorrect*] The orange flower was the rainbow butterfly's favorite. The butterfly fed from the orange flower most of the time, meaning the orange flower was the CORRECT flower most of the time."

> [*If participants answered incorrectly, experimenters ensured participants understood the task and allowed them to practice again if they wished.*]

Appendix D: Instructions for the Test Phase of the Reinforcement Learning Task

"You will now see the same 8 butterflies and the same 4 flowers that you just saw while in the scanner. All of the favorite flowers for each butterfly will stay the same, but the computer won't tell you if you are right or wrong. Your job is still to try to predict which flower each butterfly will feed from. You will see each butterfly multiple times. Press "1" to select the flower on the left side of the screen. Press "2" to select the flower on the right side of the screen."

Appendix E: Instructions for the Memory Test of the Reinforcement Learning Task

"This is the final part of the butterfly game. It involves a surprise memory test. We never fold you that you were going to do this, so just try the best you can. In the game you just played in the scanner, you saw pictures of different objects and animals. Now, you'll see some objects and animals on the screen. Your job is to try to remember whether or not you saw each picture in the scanner. If you saw the image in the scanner, press "1" to indicate that it is an OLD picture. If you did not see the image in the scanner, press "2" to indicate that it is a NEW picture.

Then, you will indicate how confident you are about your choice. You can press buttons "1", "2", "3", or "4" to indicate how confident you are about whether the image was old or new. You should press "1" if you are just guessing about your choice. You should press "2" if you are pretty sure about your choice. You should press "3" if you are very sure about your choice. You should press "4" if you are completely certain about your choice."

Appendix F: Images of Objects Used in the Learning Phase and Memory Task

VII. References

Adcock, R. A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., & Gabrieli, J. D. E. (2006). Reward-motivated learning: Mesolimbic activation precedes memory formation. *Neuron*, *50*(3), 507–517. https://doi.org/10.1016/j.neuron.2006.03.036

Aron, A., Aron, E. N., & Smollan, D. (1992). Inclusion of Other in the Self Scale and the structure of interpersonal closeness. *Journal of Personality and Social Psychology*, *63*(4), 596–612. https://doi.org/10.1037/0022-3514.63.4.596

Brown, S. L., Nesse, R. M., Vinokur, A. D., & Smith, D. M. (2003). Providing social support may be more beneficial than receiving it: Results from a prospective study of mortality. *Psychological Science*, *14*(4), 320–327. https://doi.org/10.1111/1467-9280.14461

Bunzeck, N., Dayan, P., Dolan, R. J., & Duzel, E. (2010). A common mechanism for adaptive scaling of reward and novelty. *Human Brain Mapping*, *31*(9), 1380–1394. https://doi.org/10.1002/hbm.20939

Cantin, E., Tanamachi, B., & Openshaw, H. (1999). Role for gamma interferon in control of herpes simplex virus type 1 reactivation. *Journal of Virology*, *73*(4), 3418–3423.

Carlo, G., Eisenberg, N., & Knight, G. P. (1992). An objective measure of adolescents' prosocial moral reasoning. *Journal of Research on Adolescence*, *2*(4), 331–349. https://doi.org/10.1207/s15327795jra0204_3

Casey, B. J. (2015). Beyond simple models of self-control to circuit-based accounts of adolescent behavior. *Annual Review of Psychology*, *66*(1), 295–319. https://doi.org/10.1146/annurev-psych-010814-015156

Casey, B. J., Getz, S., & Galván, A. (2008). The adolescent brain. *Developmental Review*, *28*(1), 62–77. https://doi.org/10.1016/j.dr.2007.08.003

Christakou, A., Gershman, S. J., Niv, Y., Simmons, A., Brammer, M., & Rubia, K. (2013). Neural and psychological maturation of decision-making in adolescence and young adulthood. *Journal of Cognitive Neuroscience*, *25*(11), 1807–1823. https://doi.org/10.1162/jocn_a_00447

Cohen, J. R., Asarnow, R. F., Sabb, F. W., Bilder, R. M., Bookheimer, S. Y., Knowlton, B. J., & Poldrack, R. A. (2010). A unique adolescent response to reward prediction errors. *Nature Neuroscience*, *13*(6), 669–671. https://doi.org/10.1038/nn.2558

Collins, A. G. E., & Frank, M. J. (2012). How much of reinforcement learning is working memory, not reinforcement learning? A behavioral, computational, and neurogenetic analysis. *European Journal of Neuroscience*, *35*, 1024–1035. https://doi.org/10.1111/j.1460-9568.2011.07980.x

Côté, S., Tremblay, R. E., Nagin, D., Zoccolillo, M., & Vitaro, F. (2002). The development of impulsivity, fearfulness, and helpfulness during childhood: Patterns of consistency and change in the trajectories of boys and girls. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *43*(5), 609–618. https://doi.org/10.1111/1469-7610.00050

Crone, E. A., & Dahl, R. E. (2012). Understanding adolescence as a period of social-affective engagement and goal flexibility. *Nature Reviews Neuroscience*, *13*(9), 636–650. https://doi.org/10.1038/nrn3313

Davidow, J. Y., Foerde, K., Galván, A., & Shohamy, D. (2016). An upside to reward sensitivity: The hippocampus supports enhanced reinforcement learning in adolescence. *Neuron*, *92*(1), 93–99. https://doi.org/10.1016/j.neuron.2016.08.031

Davis, M. H. (1980). A multidimensional approach to individual differences in empathy. *JSAS Catalog of Selected Documents in Psychology*, *10*, 85. https://doi.org/10.1037/0022-

3514.44.1.113

Davis, M. H. (1983). The effects of dispositional empathy on emotional reactions and helping: A multidimensional approach. *Journal of Personality*, *51*(2), 167–184. https://doi.org/10.1111/j.1467-6494.1983.tb00860.x

Dickerson, K. C., & Delgado, M. R. (2015). Contributions of the hippocampus to feedback learning. *Cognitive, Affective, & Behavioral Neuroscience*, *15*, 861–877.

Eisenberg, N., Carlo, G., Murphy, B. C., & Van Court, P. (1995). Prosocial development in late adolescence: A longitudinal study. *Child Development*, *66*(4), 1179–1197. https://doi.org/10.1037/0012-1649.27.5.849

Eisenberg, N., Cumberland, A., Guthrie, I. K., Murphy, B. C., & Shepard, S. A. (2005). Age changes in prosocial responding and moral reasoning in adolescence and early adulthood. *Journal of Research on Adolescence*, *15*(3), 235–260. https://doi.org/10.1111/j.1532-7795.2005.00095.x

Eisenberg, N., Spinrad, T. L., & Knafo-Noam, A. (2015). Prosocial Development. In R. M. Lerner (Ed.), *Handbook of Child Psychology and Developmental Science* (7th ed., pp. 1–47). John Wiley & Sons, Inc. https://doi.org/10.1002/9781118963418.childpsy315

Eisenberger, N. I. (2013). An empirical review of the neural underpinnings of receiving and giving social support: Implications for health. *Psychosomatic Medicine*, *75*(6), 545–556. https://doi.org/10.1097/PSY.0b013e31829de2e7

Eisenberger, N. I., & Cole, S. W. (2012). Social neuroscience and health: Neurophysiological mechanisms linking social ties with physical health. *Nature Neuroscience*, *15*(5), 669–674. https://doi.org/10.1038/nn.3086

Falconi, A., Gemmill, A., Dahl, R. E., & Catalano, R. (2014). Adolescent experience predicts

longevity: Evidence from historical epidemiology. *Journal of Developmental Origins of Health and Disease*, *5*(3), 171–177. https://doi.org/10.1017/S2040174414000105

Filiano, A. J., Xu, Y., Tustison, N. J., Marsh, R. L., Baker, W., Smirnov, I., Overall, C. C., Gadani, S. P., Turner, S. D., Weng, Z., Peerzade, S. N., Chen, H., Lee, K. S., Scott, M. M., Beenhakker, M. P., Litvak, V., & Kipnis, J. (2016). Unexpected role of interferon-γ in regulating neuronal connectivity and social behaviour. *Nature*, *535*(7612), 425–429. https://doi.org/10.1038/nature18626

Fine, M. S., & Minnery, B. S. (2009). Visual Salience Affects Performance in a Working Memory Task. *The Journal of Neuroscience*, *29*(25), 8016–8021. https://doi.org/10.1523/JNEUROSCI.5503-08.2009

Foerde, K., & Shohamy, D. (2011). Feedback timing modulates brain systems for learning in humans. *Journal of Neuroscience*, *31*(37), 13157–13167. https://doi.org/10.1523/JNEUROSCI.2701-11.2011

Fraser, A. M., Padilla-Walker, L. M., Coyne, S. M., Nelson, L. J., & Stockdale, L. A. (2012). Associations Between Violent Video Gaming, Empathic Concern, and Prosocial Behavior Toward Strangers, Friends, and Family Members. *Journal of Youth and Adolescence*, *41*, 636–649.

Graaff, J. Van der, Carlo, G., Crocetti, E., Koot, H. M., & Branje, S. (2017). Prosocial Behavior in Adolescence: Gender Differences in Development and Links with Empathy. *Journal of Youth and Adolescence*, *47*, 1086–1099.

Hämmerer, D., Li, S.-C., Müller, V., & Lindenberger, U. (2011). Life span differences in electrophysiological correlates of monitoring gains and losses during probabilistic reinforcement learning. *Journal of Cognitive Neuroscience*, *23*(3), 579–592.

https://doi.org/10.1162/jocn.2010.21475

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

Hare, T. A., O'Doherty, J. P., Camerer, C. F., Schultz, W., & Rangel, A. (2008). Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. *Journal of Neuroscience*, *28*(22), 5623–5630. https://doi.org/10.1523/JNEUROSCI.1309-08.2008

Huang, S., Hendriks, W., Althage, A., Hemmi, S., Bluethmann, H., Kamijo, R., Vilček, J., Zinkernagel, R. M., & Aguet, M. (1993). Immune response in mice that lack the interferon-gamma receptor. *Science*, *259*(5102), 1742–1745.

Inagaki, T. K., & Eisenberger, N. I. (2012). Neural correlates of giving support to a loved one. *Psychosomatic Medicine*, *74*, 3–7.

Jones, R. M., Somerville, L. H., Li, J., Ruberry, E. J., Libby, V., Glover, G., Voss, H. U., Ballon, D. J., & Casey, B. J. (2011). Behavioral and neural properties of social reinforcement learning. *Journal of Neuroscience*, *31*(37), 13039–13045. https://doi.org/10.1523/JNEUROSCI.2972-11.2011

Jones, R. M., Somerville, L. H., Li, J., Ruberry, E. J., Powers, A., Mehta, N., Dyke, J., & Casey, B. J. (2014). Adolescent-specific patterns of behavior and neural activity during social reinforcement learning. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(2), 683–697. https://doi.org/10.3758/s13415-014-0257-z

Keltner, D., Kogan, A., Piff, P. K., & Saturn, S. R. (2014). The Sociocultural Appraisals, Values, and Emotions (SAVE) framework of prosociality: Core processes from gene to meme.

Annual Review of Psychology, *65*(1), 425–460. https://doi.org/10.1146/annurev-psych-010213-115054

Knutson, B., Fong, G. W., Bennett, S. M., Adams, C. M., & Hommer, D. (2003). A region of mesial prefrontal cortex tracks monetarily rewarding outcomes: Characterization with rapid event-related fMRI. *NeuroImage*, *18*, 263–272.

Knutson, B., Rick, S., Wimmer, G. E., Prelec, D., & Loewenstein, G. (2007). Neural predictors of purchases. *Neuron*, *53*, 147–156.

Leschak, C. J., Dutcher, J. M., Byrne Haltom, K. E., Breen, E. C., Bower, J. E., & Eisenberger, N. I. (n.d.). *Associations between Psychosocial Factors and Circulating Cytokines in Breast Cancer Survivors*.

Leschak, C. J., & Eisenberger, N. I. (2019). Two distinct immune pathways linking social relationships with health: Inflammatory and antiviral processes. *Psychosomatic Medicine*. https://doi.org/10.1097/PSY.0000000000000685

Li, Y., & Ferraro, K. F. (2005). Volunteering and depression in later life: Social benefit or selection processes? *Journal of Health and Social Behavior*, *46*(1), 68–84. https://doi.org/10.1177/002214650504600106

Lockwood, P. L., Apps, M. A. J., Valton, V., Viding, E., & Roiser, J. P. (2016). Neurocomputational mechanisms of prosocial learning and links to empathy. *Proceedings of the National Academy of Sciences*, *113*(35), 9763–9768. https://doi.org/10.1073/pnas.1603198113

Luengo Kanacri, B. P., Pastorelli, C., Eisenberg, N., Zuffianò, A., & Caprara, G. V. (2013). The development of prosociality from adolescence to early adulthood: The role of effortful control. *Journal of Personality*, *81*(3), 302–312. https://doi.org/10.1111/jopy.12001

Masten, C. L., Eisenberger, N. I., Borofsky, L. A., McNealy, K., Pfeifer, J. H., & Dapretto, M. (2011). Subgenual anterior cingulate responses to peer rejection: A marker of adolescents' risk for depression. *Development and Psychopathology*, *23*(1), 283–292. https://doi.org/10.1017/S0954579410000799

Masten, C. L., Eisenberger, N. I., Borofsky, L. A., Pfeifer, J. H., McNealy, K., Mazziotta, J. C., & Dapretto, M. (2009). Neural correlates of social exclusion during adolescence: Understanding the distress of peer rejection. *Social Cognitive and Affective Neuroscience*, *4*(2), 143–157. https://doi.org/10.1093/scan/nsp007

Masten, C. L., Morelli, S. A., & Eisenberger, N. I. (2011). An fMRI investigation of empathy for "social pain" and subsequent prosocial behavior. *NeuroImage*, *55*, 381–388.

Mayberg, H. S., Lozano, A. M., Voon, V., McNeely, H. E., Seminowicz, D., Hamani, C., Schwalb, J. M., & Kennedy, S. H. (2005). Deep brain stimulation for treatment-resistant depression. *Neuron*, *45*(5), 651–660. https://doi.org/10.1016/J.NEURON.2005.02.014

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), 1038–1045. https://doi.org/10.1177/0956797615578476

Moll, J., Krueger, F., Zahn, R., Pardini, M., de Oliveira-Souza, R., & Grafman, J. (2006). Human fronto-mesolimbic networks guide decisions about charitable donation. *Proceedings of the National Academy of Sciences*, *103*(42), 15623–15628. https://doi.org/10.1073/pnas.0604475103

Morelli, S. A., Rameson, L. T., & Lieberman, M. D. (2014). The neural components of empathy: Predicting daily prosocial behavior. *Social Cognitive and Affective Neuroscience*, *9*(1), 39–47. https://doi.org/10.1093/scan/nss088

Morrow-Howell, N., Hinterlong, J., Rozario, P. A., & Tang, F. (2003). Effects of volunteering on the well-being of older adults. *The Journals of Gerontology: Series B*, *58*(3), S137–S145. https://doi.org/10.1093/geronb/58.3.S137

Müller, U., Steinhoff, U., Reis, L. F. L., Hemmi, S., Pavlovic, J., Zinkernagel, R. M., & Aguet, M. (1994). Functional role of type I and type II interferons in antiviral defense. *Science*, *264*(5167), 1918–1921. https://doi.org/10.1126/science.8009221

Musick, M. A., Herzog, A. R., & House, J. S. (1999). Volunteering and mortality among older adults: Findings from a national sample. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *54B*(3), S173–S180. https://doi.org/10.1093/geronb/54B.3.S173

Nelson-Coffey, S. K., Fritz, M. M., Lyubomirsky, S., & Cole, S. W. (2017). Kindness in the blood: A randomized controlled trial of the gene regulatory impact of prosocial behavior. *Psychoneuroendocrinology*, *81*, 8–13. https://doi.org/10.1016/j.psyneuen.2017.03.025

Nelson, E. E., Leibenluft, E., McClure, E. B., & Pine, D. S. (2005). The social re-orientation of adolescence: A neuroscience perspective on the process and its relation to psychopathology. *Psychological Medicine*, *35*(2), 163–174. https://doi.org/10.1017/S0033291704003915

O'Doherty, J. P., Dayan, P., Friston, K., Critchley, H., & Dolan, R. J. (2003). Temporal difference models and reward-related learning in the human brain. *Neuron*, *38*(2), 329–337. https://doi.org/10.1016/S0896-6273(03)00169-7

Papageorgiou, G. K., Baudonnat, M., Cucca, F., & Walton, M. E. (2016). Mesolimbic dopamine encodes prediction errors in a state-dependent manner. *Cell Reports*, *15*(2), 221–228. https://doi.org/10.1016/j.celrep.2016.03.031

Peirce, J. W. (2007). PsychoPy—Psychophysics software in Python. *Journal of Neuroscience*

Methods, *162*(1–2), 8–13. https://doi.org/10.1016/j.jneumeth.2006.11.017

Ploghaus, A., Tracey, I., Clare, S., Gati, J. S., Rawlins, J. P. N., & Matthews, P. M. (2000). Learning about pain: The neural substrate of the prediction error for aversive events. *Proceedings of the National Academy of Sciences*, *97*(16).

Rameson, L. T., Morelli, S. A., & Lieberman, M. D. (2011). The neural correlates of empathy: Experience, automaticity, and prosocial behavior. *Journal of Cognitive Neuroscience*, *24*(1), 235–245.

Ramirez-Mahaluf, J. P., Perramon, J., Otal, B., Villoslada, P., & Compte, A. (2018). Subgenual anterior cingulate cortex controls sadness-induced modulations of cognitive and emotional network hubs. *Scientific Reports*, *8*(1), 8566. https://doi.org/10.1038/s41598-018-26317-4

Saxena, S., Brody, A. L., Ho, M. L., Zohrabi, N., Maidment, K. M., & Baxter, L. R. (2003). Differential brain metabolic predictors of response to paroxetine in obsessive-compulsive disorder versus major depression. *American Journal of Psychiatry*, *160*(3), 522–532. https://doi.org/10.1176/appi.ajp.160.3.522

Schreier, H. M. C., Schonert-Reichl, K. A., & Chen, E. (2013). Effect of volunteering on risk factors for cardiovascular disease in adolescents. *JAMA Pediatrics*, *167*(4), 327–332. https://doi.org/10.1001/jamapediatrics.2013.1100

Schreuders, E., Klapwijk, E. T., Will, G.-J., & Güroğlu, B. (2018). Friend versus foe: Neural correlates of prosocial decisions for liked and disliked peers. *Cognitive, Affective, & Behavioral Neuroscience*, *18*(1), 127–142. https://doi.org/10.3758/s13415-017-0557-1

Schultz, W., Dayan, P., & Montague, P. R. (1997). A neural substrate of prediction and reward. *Science*, *275*(5306), 1593–1599. https://doi.org/10.1126/science.275.5306.1593

Soto, C. J., John, O. P., Gosling, S. D., & Potter, J. (2011). Age differences in personality traits

from 10 to 65: Big Five domains and facets in a large cross-sectional sample. *Journal of Personality and Social Psychology*, *100*(2), 330–348. https://doi.org/10.1037/a0021717

Spear, L. P. (2000). The adolescent brain and age-related behavioral manifestations. *Neuroscience and Biobehavioral Reviews*, *24*(4), 417–463. https://doi.org/10.1016/S0149-7634(00)00014-2

Steinberg, L. (2008). A social neuroscience perspective on adolescent risk-taking. *Developmental Review*, *28*(1), 78–106. https://doi.org/10.1016/j.dr.2007.08.002

Sutton, R. S., & Barto, A. G. (Eds.). (2017). *Reinforcement Learning: An Introduction* (2nd ed.). The MIT Press.

Taylor, S. J., Barker, L. A., Heavey, L., & McHale, S. (2013). The typical developmental trajectory of social and executive functions in late adolescence and early adulthood. *Developmental Psychology*, *49*(7), 1253–1265. https://doi.org/10.1037/a0029871

Telzer, E. H., Fuligni, A. J., Lieberman, M. D., & Galván, A. (2013). Ventral striatum activation to prosocial rewards predicts longitudinal declines in adolescent risk taking. *Developmental Cognitive Neuroscience*, *3*(1), 45–52. https://doi.org/10.1016/j.dcn.2012.08.004

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., & Joliot, M. (2002). Automated anatomical labeling of activiations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *NeuroImage*, *15*, 273–289.

Van Den Bos, W., Cohen, M. X., Kahnt, T., & Crone, E. A. (2012). Striatum-medial prefrontal cortex connectivity predicts developmental changes in reinforcement learning. *Cerebral Cortex*, *22*(6), 1247–1255. https://doi.org/10.1093/cercor/bhr198

Van Der Meulen, M., Van Ijzendoorn, M. H., & Crone, E. A. (2016). Neural correlates of

prosocial behavior: Compensating social exclusion in a four-player Cyberball game. *PLOS One*, *11*(7), e0159045. https://doi.org/10.1371/journal.pone.0159045

Van Goethem, A., Van Hoof, A., Orobio de Castro, B., Van Aken, M., & Hart, D. (2014). The role of reflection in the effects of community service on adolescent development: A meta-analysis. *Child Development*, *85*(6), 2114–2130. https://doi.org/10.1111/cdev.12274

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

Wimmer, G. E., & Shohamy, D. (2012). Preference by association: How memory mechanisms in the hippocampus bias decisions. *Science*, *338*(6104), 270–273. https://doi.org/10.1126/science.1223252

Yang, T. T., Simmons, A. N., Matthews, S. C., Tapert, S. F., Frank, G. K., Bischoff-Grethe, A., Lansing, A. E., Wu, J., Brown, G. G., & Paulus, M. P. (2009). Depressed adolescents demonstrate greater subgenual anterior cingulate activity. *Neuroreport*, *20*(4), 440. https://doi.org/10.1097/WNR.0B013E3283262E10

Zahn, R., de Oliveira-Souza, R., Bramati, I. E., Garrido, G., & Moll, J. (2009). Subgenual cingulate activity reflects individual differences in empathic concern. *Neuroscience Letters*, *457*(2), 107–110. https://doi.org/10.1016/J.NEULET.2009.03.090

Zahn, R., Moll, J., Paiva, M., Garrido, G., Krueger, F., Huey, E. D., & Grafman, J. (2009). The neural basis of human social values: Evidence from functional MRI. *Cerebral Cortex*, *19*(2), 276–283. https://doi.org/10.1093/cercor/bhn080