Learning together: behavioral, computational, and neural mechanisms underlying social learning in adolescence
Westhoff, B.

LEARNING TOGETHER

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Printed by Ipskamp Printing | proefschriften.net
Layout and design: Erwin Timmerman, persoonlijkproefschrift.nl

Cover design
Harma Makken, persoonlijkproefschrift.nl

ISBN
978-94-6421-655-4

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Proefschrift

ter verkrijging van
de graad van doctor aan de Universiteit Leiden,
op gezag van rector magnificus prof.dr.ir. H. Bijl,
volgens besluit van het college voor promoties
te verdedigen op dinsdag 5 april 2022
klokke 13:45 uur

door

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geboren te Amsterdam
in 1992

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The research described in this thesis was supported by an Open Research Area (ORA) grant (464-15-176) from The Netherlands Organization for Scientific Research (NWO) awarded to dr. Anna C.K. van Duijvenvoorde.

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Chapter 1

General Introduction

The scope of this thesis

When you think about things you have learned as a child or teenager, you will likely think about particular skills or something you learned from (school) books, such as reading, math, or riding a bike. However, humans are sophisticated social beings who live in a dynamic and complex social environment, and encounter numerous social situations daily. Therefore, a considerable part of what we learn is *social* information, enabling us to navigate the social environment. For example, social interactions require quick learning about the behavior of other people. For instance, when you think about the first day of high school, you may recall this as an exciting day in which you were going to meet many new people. You did not know (most of) them yet: who were you going to like or dislike? Who would be your friends? Who would be your ideal project buddy? You had to learn about these people, which involves predicting others' behavior and interacting successfully with them. These are important elements of *social learning*.

Social learning thus involves predictions about other people – which affect your upcoming choices or actions – and these predictions will be updated when they do not match the actual outcome. Social learning may take different forms, which differ in the information one learns and its purpose. Historically, social learning theory was proposed by Albert Bandura (Bandura, 1977), which defines social learning as learning without direct reinforcement, such as learning *from* others by observing, imitating, and modeling their behavior, or vicariously learning from others' actions and outcomes (rewards and punishments). In addition, as mentioned above, social learning can involve learning *about* other people, such as whether you can or cannot trust someone. Finally, social learning may also encompass learning *for* others. That is, many of our actions may affect other people and we have to learn which actions we should repeat to help others. For example, to comfort an upset friend, we need to know what actions cheer them up. Learning to benefit or help others can also be referred to as *prosocial learning* (Lockwood et al., 2016). The current thesis focusses on learning *about* and learning *for* others. Although these two forms of social learning differ, they have overlapping elements and generally encompass learning about actions and their outcomes which involve other people.

Being able to learn adaptively in a social context is an essential social skill (Fareri et al., 2020). Social learning skills enable you, for instance, to know who you can/should cooperate with (e.g., in school or business projects), who you can trust with your secrets, and how best to help someone. Thus, the ability to learn about and for others helps you make appropriate choices that involve others, and determine how to behave around other people. Adaptive social skills are vital for building and maintaining healthy social relationships (Fareri et al., 2020), which have been shown to be beneficial for one's long-term wellbeing (Güroğlu, 2021; Uchino, 2009).

Social learning is a complex social skill that develops and improves across development. A developmental period that has been suggested to be particularly key for developing social learning skills, is adolescence (Blakemore & Mills, 2014; Crone & Dahl, 2012). Adolescence is a sensitive period for social development in general, and is characterized by large changes in the social environment. That is, adolescents spend more time with peers than with their family, and their social relations become more intense and complex (Brown & Larson, 2009; De Goede et al., 2009; Lam et al., 2014). Moreover, their sensitivity to social stimuli is heightened, which may, for example, result in increased susceptibility to peer influence (Blakemore & Mills, 2014; Crone & Dahl, 2012; Foulkes & Blakemore, 2016). These psychosocial changes are thought to result from ongoing structural and functional changes in the brain (Blakemore & Mills, 2014; Nelson et al., 2016; Somerville, 2013). Due to these environmental and neurobiological changes, adolescence may be a life phase particularly attuned to social learning.

In this thesis, I aim to examine the development of two forms of social learning across adolescence. Here, I will focus on (1) learning *about* other people, specifically, whether they are (un)cooperative and (un)trustworthy, and (2) learning *for* other people (prosocial learning) to know what actions may help others. To this end, I make use of multiple experimental paradigms in samples spanning early adolescence to late adolescence. A second aim was to examine underlying mechanisms and factors that account for age-related and individual differences in social learning. To this end, I combined self-report questionnaires, computational modeling, and functional neuroimaging.

In this first chapter, I first provide an introduction about adolescence as a key period for social development. Here, I discuss two social behaviors - specifically, trust behavior and prosocial behavior - that play an important role in social interactions as well as in the different forms of social learning. Next, I present reinforcement learning as a framework for social learning. Finally, I highlight the added value of using economic games, computational modeling, and functional neuroimaging for studying social decision-making and learning, and end with an outline of the empirical chapters.

Adolescence as a key phase for developing social learning skills

Adolescence is the developmental phase that marks the transition from childhood to adulthood. Adolescence has a biological starting point with the onset of puberty and accompanying hormonal and biological changes (+/- 9-12 years old) (Spear, 2011). The end of adolescence is culturally determined, but in Western cultures this is generally when one reaches mature social goals and is relatively independent of their parents. Thus, adolescence roughly spans 9-24 years of age, although different ages or (sub)labels are being used (Sawyer et al., 2018).

Adolescence is characterized by biological changes in levels of pubertal hormones, physical characteristics, and brain anatomy and function (see e.g., Dumontheil, 2016). Besides these biological changes, however, this life phase is also a time of profound psychological and social changes. Adolescence is a time of social reorientation, during which the social world and peer interactions become increasingly important. For instance, adolescents spend more time with peers than in childhood (De Goede et al., 2009), both offline and online (Lam et al., 2014), and they form and maintain high-quality friendships (Brown & Larson, 2009). Concurrently, there is a heightened sensitivity to social stimuli (Foulkes & Blakemore, 2016; Somerville, 2013) which may, for example, result in increased attention to peer evaluation (Guyer et al., 2014) and an increased susceptibility to peer influence (Blakemore & Mills, 2014; Crone & Dahl, 2012; Foulkes & Blakemore, 2016). Moreover, both the quantity and quality of social interactions change, and for functioning as an adult and achieving mature levels of social competence, it is essential that adolescents develop adaptive social skills. These are needed for e.g., building reciprocal social relations, which have been shown to be essential for long-term health and (emotional) wellbeing (Baumeister & Leary, 1995; House et al., 1988). In sum, adolescence is a key life phase for developing well-adjusted social behavior.

Well-adjusted social behavior comprises of multiple adaptive social learning skills. Next, I will discuss trust behavior and prosocial behavior, as these social behaviors play an important role in social interactions, as well as in learning about and learning for others, respectively.

Trust

A crucial component for cooperative social interactions and mutually beneficial interpersonal relationships, is trust. Trust is important at all levels of society – from interpersonal to institutional trust – and well-adjusted social behavior therefore also entails being adaptive with regard to deciding whether or not to trust. That is, trusting others who will reciprocate your trust will result in positive social interactions. However, trusting others who will betray your trust, will be wasteful for your resources. Showing maladaptive trust decisions, i.e., both trusting too often or too little, is likely to result in problems with peer relations and social behavior (Rotenberg et al., 2005). Therefore, it is vital for successfully navigating the social environment to be able to learn whom you can or cannot trust.

For studying social decision-making behaviors such as trust, economic games are well-suited. Economic games allow studying complex processes in a controlled experimental setup, and are moreover suitable for studying developmental patterns across large age ranges (Camerer, 2003; Gummerum et al., 2008). A well-known economic game for studying trust, is the trust game. In the original trust game, participants may have the role as either an investor or a trustee (Berg et al., 1995). As the investor, a participant may have two options: trusting (i.e., investing) or not trusting (i.e., not investing) the trustee. When choosing to trust, the investment (e.g., coins or tokens) will be multiplied with a certain factor, and the trustee can decide how much to reciprocate to the investor. Choosing to trust the trustee may result in the highest possible outcome in this game, but only if the trustee will actually behave trustworthy (i.e., reciprocate). Choosing not to trust the other will result in a guaranteed outcome, yet lower than a reciprocated trust choice. Choosing not to trust is optimal when the trustee is indeed untrustworthy, but choosing not to trust someone that turned out to be trustworthy, will result in a suboptimal outcome. Previous research has used (variations on) the trust game for studying developmental patterns of trust behavior across adolescence. These studies reported increasing levels of trust behavior from early- to mid-adolescence (e.g., (Fett, Gromann, et al., 2014; Sutter & Kocher, 2007; van den Bos et al., 2010; van den Bos, van Dijk, et al., 2012).

In the current thesis, chapters 2-4 use experimental paradigms that are based on these trust game principles to study adolescents' ability to learn about the trustworthiness of others (chapters 2 and 3), and, more specifically, how they sample information on others' trustworthiness in order to decide whether to trust someone (chapter 4).

Prosocial behaviors

Another form of social behavior that plays an important role in social relations, is prosocial behavior. Prosocial behaviors are defined as voluntary social behaviors that are intended to benefit others (Padilla-Walker & Carlo, 2014). It is a multidimensional construct that involves a wide variety of behaviors, such as helping others, sharing resources, cooperating, and comforting. Studies have shown that prosocial behavior is important for being liked by others, and building and maintaining positive reciprocal social relationships (Güroğlu et al., 2007; Peters et al., 2010). With regard to developmental patterns of prosocial behavior, studies have shown that across age, adolescents increasingly exhibit prosocial behaviors in the domain of sharing and giving (Güroğlu et al., 2014; Padilla-Walker & Carlo, 2014).

To be able to show prosocial behaviors, it is essential that you are able to learn which of your actions have beneficial consequences for the other person (i.e., prosocial learning). Previous studies investigating prosocial learning, have used prosocial learning tasks in which participant could learn to obtain rewards for others (prosocial learning), and distinguished that from self-benefitting learning (Cutler et al., 2021; Lockwood et al., 2016; Sul et al., 2015). Although numerous developmental studies on prosocial behavior have been conducted in the past years (e.g., Güroğlu et al., 2014; Schreuders et al., 2018; van de Groep et al., 2020; van Hoorn et al., 2016), no studies have investigated prosocial *learning* across development. In chapter 5, I used such a prosocial learning task to investigate age-related differences in adolescents' abilities to learn for others compared to learning for self.

Reinforcement learning framework applied to social learning

A framework of interest to understand the mechanisms of social learning, is reinforcement learning (Figure 1A). Reinforcement learning enables describing how decisions and their outcomes are paired over time (Sutton & Barto, 1998). This reinforcement learning framework can be captured in a mathematical framework, which has been widely applied in many areas of psychology and neuroscience (Dayan & Balleine, 2002; Zhang et al., 2020). Reinforcement learning is a process in which our past experiences are used to perform actions that are likely to result in positive outcomes. Reinforcement learning depends largely on *prediction errors* (PEs), which reflect the difference between the expected outcome and actual outcome of an action. When the outcome is better or worse than expected, there is a PE, and its size depends on how large the deviation is. PEs drive learning as they are used to update the future expectation with the new information. That is, an outcome that is better than expected (positive PE), will increase our expectations that performing that action again will result in a positive outcome, and we will become more likely to repeat the action in the future. When an outcome is worse than expected (negative PE), we update our expectations as such that we will be more likely to avoid that action in the future. The extent to which expectations are updated is determined by a *learning rate*. For someone with a relatively high learning rate, the weight of the PE is larger and their expectations are being updated to a greater extent. For someone with a rather low learning rate, however, the weight of a PE is lower and their expectations are updated only to a limited extent. As a result, they incorporate the feedback not only from the last situation but from a longer time frame, which could e.g., be beneficial in relatively stable learning contexts (Nussenbaum & Hartley, 2019).

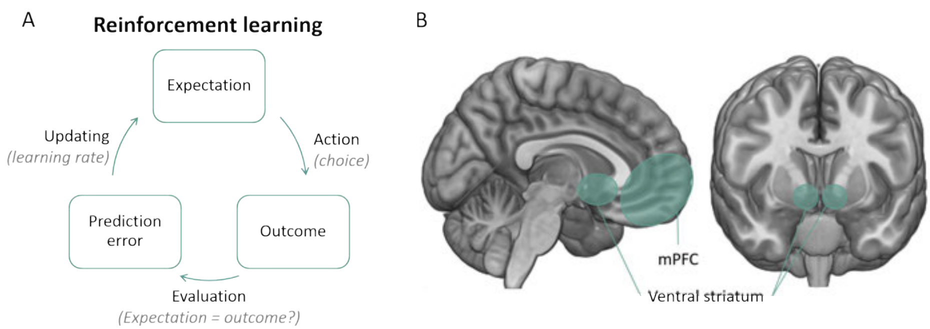


Figure 1. (A) Reinforcement learning framework. The action you perform is based on your expectation of the resulting outcome. During the evaluation, the actual outcome of your action is compared to your expected outcome. The difference between these, is the prediction error. A prediction error of 0 indicates that the outcome precisely matches your expectations. If the actual outcome differs from your expected outcome (prediction error ≠ 0), this will be used to update your expectations for the

subsequent action. The extent to which you update your expectations is determined by your learning rate. **(B)** Ventral striatum and medial prefrontal cortex (mPFC) are core brain regions involved in reinforcement learning.

For using the reinforcement learning framework to investigate (social) learning, researchers make use of computational modeling. Computational models are mathematical models applied to behavioral data. The advantage of such a computational model is that they can describe behavior, and as such can identify underlying mechanisms that you cannot directly observe or measure from behavior (i.e., latent variables) (van den Bos et al., 2018). Therefore, computational modeling is a valuable tool for studying people's behavior and the underlying mechanisms of individual or developmental differences therein.

A novel perspective is to apply this reinforcement learning framework to social learning, as it is thought to rely, at least partly, on similar computational learning mechanisms (Joiner et al., 2017; Lockwood & Klein-Flügge, 2020; Zhang et al., 2020) and potentially also similar neural mechanisms (Lockwood et al., 2020) as those used in basic reinforcement learning. For example, computational reinforcement learning models in social learning contexts have assessed whether learning rates differ between learning conditions (e.g., learning to benefit oneself compared to learning to benefit others (Cutler et al., 2021; Lockwood et al., 2016). However, in social psychology and neuroscience, variations on these reinforcement learning models may be insightful as well (Zhang et al., 2020). For instance, these reinforcement learning models can be extended with social elements, such as social preferences (inequality aversion), to better capture the underlying processes involved in social learning.

In this thesis, I applied computational modeling to study how adolescents learn *about* and *for* other people, and examined developmental and individual differences in the underlying computational mechanisms of social learning.

Social reinforcement learning in the developing brain

An additional valuable methodological approach for understanding underlying mechanisms of a particular behavior, is the use of functional neuroimaging. When studying the brain, researchers often make use of Magnetic Resonance Imaging (MRI) scanners. This noninvasive method is suitable to use in participants from a relatively young age. When the MRI scanner is used to measure the blood-oxygen-level dependent (BOLD) signal in the blood vessels in the brain, this is called functional MRI (fMRI). These oxygen levels are an indirect measure of neural activity: when neurons in a certain brain area are active, they will need oxygen, thus higher oxygenated levels indirectly indicate more activity in that particular brain area. When participants perform a task (e.g., a social learning task) during fMRI, the scanner takes images every few seconds. This technique allows researchers to study which brain areas are involved during which parts of the tasks. fMRI has a good spatial resolution, which allows locating the BOLD signals during specific tasks or events.

fMRI has been used across an extensive range of experimental paradigms. For studies on (social) learning fMRI can add insights in what neurobiological mechanisms underlie reinforcement learning. When this is combined with computational modeling, this allows for more sophisticated probing of the learning processes. That is, the PEs (representing learning signals) are extracted on a trial-by-trial basis from the computational models. These PEs can be used in the fMRI analyses such that the learning signals can be tracked in the brain. Key regions that have been linked to reinforcement learning are the ventral striatum and the medial prefrontal cortex (mPFC) (see Figure 1B). The striatum is a region located in the mid-brain that receives dopaminergic input from the ventral tegmental area and substantia nigra, and is functionally related to reward processing and (social) learning (Olsson et al., 2020). The striatum has connections with the mPFC. The mPFC is thought to integrate reward (value) and is involved in (social) decision-making and reinforcement learning (Joiner et al., 2017). Although social learning may depend on several interacting brain regions, these reward-related regions are expected to be key for social learning.

Thus, using fMRI for studying social learning provides insights into its underlying mechanisms. In chapter 5, I combined fMRI with computational modeling of prosocial learning data, and examined age-related differences in prosocial learning signals in the ventral striatum and mPFC.

Outline of this thesis

In this thesis, I report the results from four empirical studies that I have conducted to investigate the development and underlying mechanisms of social learning in typically developing adolescents, using experimental behavioral paradigms, self-report questionnaires, computational modeling, and fMRI.

In **chapter 2**, I present an experimental paradigm consisting of multiple 1-shot economic games to examine adolescents' ability to learn *about* and adjust to others that differed in their levels of cooperative behaviors (i.e., trustworthiness and cooperation). More specifically, in one condition ('trust game') participants had to learn to trust trustworthy others and not trust untrustworthy others. In the other condition ('coordination game'), participants had to learn to coordinate their choices by accepting either an advantage from cooperative others or a disadvantage from uncooperative others. In a large adolescent sample spanning a broad age range (N = 244, 8-23 years), I examined age-related differences and factors (e.g., learning rates) underlying individual differences in participants' ability to learn to adjust to others' behavior.

Chapter 3, describes an experimental study in an adolescent sample with a broad age range (*N* = 157, 10-24 years) that focused on the trust game condition from chapter 2. I expanded this paradigm by adding a reversal learning manipulation in which the others' behavior reversed unannouncedly. Assessing participants' reversal-learning abilities provide insights into how flexibly adolescents can adjust their behavior towards changing levels of others' trustworthiness. Additionally, a non-social version of the task was included to assess whether there are differences between social and non-social trust learning. I aimed to study age-related differences in participants' social and non-social trust learning and trust reversal-learning abilities, and additionally assessed factors underlying individual differences that may affect their social learning abilities.

Chapter 4, builds on the findings from chapter 2 and 3, and describes a study that further examined how adolescents sample information on others' past trust behavior when they have to decide whether to trust them. In a trust sampling paradigm, participants could sample information about the trustworthiness of peers, ranging from always trustworthy to always untrustworthy, before they decide to trust or not (*N* = 157, 10-24 years, same sample as in chapter 3). Using computational modeling, I examined age-related differences in how adolescents used this information to update their beliefs about others' trustworthiness. Together, this setup elaborates on the underlying cognitive processes involved in trusting behavior.

In **chapter 5**, I describe an fMRI study in adolescents (*N* = 74, 9-21 years) in which I examined another type of social learning: prosocial learning. Here, I aimed to investigate how adolescents learn to obtain positive outcomes for self versus for others. By combining computational modeling with functional neuroimaging, I was able to assess in prosocial learning signals in the brain. With this study, I thus aimed to examine age-related and individual differences in prosocial learning on both a behavioral and neural level.

Finally, in **chapter 6** I summarize the results of the empirical studies in this thesis, and provide an overall discussion of the findings and its implications.

2

Chapter 2

Developmental asymmetries in learning to adjust to cooperative and uncooperative environments

This chapter is published as:
Westhoff, B., Molleman, L., Viding, E., van den Bos, W., & van Duijvenvoorde, A. C. K. (2020). Developmental asymmetries in learning to adjust to cooperative and uncooperative environments. *Scientific Reports*, *10*(1), 21761. https://doi.org/10.1038/s41598-020-78546-1

Abstract

Learning to successfully navigate social environments is a critical developmental goal, predictive of long-term wellbeing. However, little is known about how people learn to adjust to different social environments, and how this behavior emerges across development. Here, we use a series of economic games to assess how children, adolescents, and young adults learn to adjust to social environments that differ in their level of cooperation (i.e., trust and coordination). Our results show an asymmetric developmental pattern: adjustment requiring uncooperative behavior remains constant across adolescence, but adjustment requiring cooperative behavior improves markedly across adolescence. Behavioral and computational analyses reveal that age-related differences in this social learning are shaped by age-related differences in the degree of inequality aversion and in the updating of beliefs about others. Our findings point to early adolescence as a phase of rapid change in cooperative behaviors, and highlight this as a key developmental window for interventions promoting well-adjusted social behavior.

Introduction

Humans have evolved in a highly social environment in which they continuously make decisions about how to engage with others. Well-adjusted social behavior requires individuals to learn whom they can trust and cooperate with. We typically trust others whom we expect to reciprocate that trust in the future, and beliefs about others' trustworthiness are updated through everyday experiences. For example, if a friend violates our trust, this calls for an adjustment of our belief in their trustworthiness. This may not happen on the first violation, but if this friend continues their untrustworthy behavior, the friendship is unlikely to survive. Adjusting our beliefs based on outcomes of social interactions enables decision making that matches the situation and can be critical for successful navigation of the social world. In line with this notion, well-adjusted social behavior has been linked to positive developmental trajectories (e.g., in health, education, and social development), and is important for long-term mental health (Crone & Dahl, 2012; Dahl et al., 2018; Paus et al., 2008; Sawyer et al., 2018). With the rise of complex social worlds (both online and offline), learning about and adjusting to different social environments may be more important than ever. Yet little is known about the factors that underlie learning and adjusting in social environments, and how these skills manifest across adolescence.

Mounting evidence suggests that adolescence – the period between childhood and young adulthood – is a life phase in which learning and flexible behavior mature rapidly (see e.g., (Blakemore & Mills, 2014; Casey et al., 2008; Crone & Dahl, 2012; Sawyer et al., 2018). Moreover, adolescence is marked by a social reorientation: individuals start to form larger peer groups, peers gain in importance compared with parents, and social interactions become more complex (Chein et al., 2011; Larson & Richards, 1991; Larson et al., 1996; van Hoorn et al., 2016). Adolescence is, therefore, an important life phase for developing well-adjusted social behavior, with cooperative and uncooperative behaviors becoming more salient as adolescents deal with their social environments more independently. Developmental research into social decision making has shown that from an early age, children trust others and recognize that investing in others can lead to mutual benefits (Rosati et al., 2019). Cooperative behaviors, such as trust and prosocial behavior, are thought to continuously increase during adolescence (Blakemore & Mills, 2014; Eisenberg et al., 1991, 1995; van den Bos et al., 2010) (but see House et al., (2020)). A more nuanced view is that adolescents do not show more cooperative behaviors per se, but instead increasingly tailor their behavior to the social environment. For example, when undertaking prosocial actions they increasingly differentiate between friends and strangers (Fett, Shergill, et al., 2014; Güroğlu et al., 2014; van de Groep et al., 2020). Also, adolescents learn to adjust to interaction partners that differ in their level of trustworthiness (van den Bos, van Dijk, et al., 2012), something that children find difficult (Rosati et al., 2019).

Theoretically, decisions to cooperate can be based on at least three distinctive factors, each of which could differ between individuals and could contribute to developmental differences in adjusting behavior in social contexts: (1) social preferences, (2) prior expectations, and (3) updating of expectations. First, *social preferences* refer to individuals caring about relative outcomes, i.e. disliking having either a better or worse outcome than others (Fehr & Schmidt, 1999). Such social preferences show changes across development (see McAuliffe et al., (2017) for a review).The preference of avoiding getting *less* than others (i.e., disadvantageous inequality aversion) increases from age 4 to early adolescence (Fehr et al., 2008), which has been shown across many cultures (Blake et al., 2015), before it decreases again across adolescence (Meuwese et al., 2015). On the other hand, the preference of avoiding getting *more* than others (i.e., advantageous inequality aversion), appears from about 8 years old (Blake & McAuliffe, 2011; Fehr et al., 2008), and has been suggested to decrease across adolescence, particularly for boys (Meuwese et al., 2015). Nonetheless, also in adulthood people exhibit disadvantageous and advantageous inequality aversion (e.g., Dawes et al., 2007; Fehr & Schmidt, 1999). Although this evidence suggests that social preferences continue to develop across adolescence, little is known about how they impact learning in social environments. For instance, high levels of disadvantageous inequality aversion could prevent cooperative behavior due to a fear of getting less than others, even if there is a relatively strong expectation that others will cooperate.

Second, *prior expectations* (i.e., descriptive norms, the perceptions of what most people do (Chang & Sanfey, 2013; Delgado et al., 2005; Ruff & Fehr, 2014) inform decision making by generating predictions about the behavior of others (e.g., I will cooperate if this person is likely to reciprocate). Individual differences in initial expectations about others may lead to individual differences in choices (Fareri et al., 2015), and it is conceivable that different age groups have varying prior expectations (Ma, Westhoff, et al., 2020). However, prior expectations have hardly been studied in developmental populations, despite being important determinants of cooperative behaviors.

Third, adjusting behavior requires expectations to be *updated* in response to new information. Updating of expectations in social environments can be captured by reinforcement learning (RL) models (e.g., Cheong et al., 2017; Hackel et al., 2019; van den Bos et al., 2013), in which learning is driven by differences between expected and received rewards (i.e., prediction errors). Adolescence is characterized by substantial improvements in flexible learning and quick adaptation to novel non-social contexts (Decker et al., 2015; Hauser et al., 2015; van den Bos, Cohen, et al., 2012); whether this extends to the social domain, however, is still unclear (but see Rosenblau et al., (2018)).

Here we examine experimentally how children, adolescents, and adults adjust to social environments that differ in their level of cooperation, and aim to provide a mechanistic explanation by evaluating the role of social preferences, prior expectations, and expectation updating. To achieve this goal, we deployed a set of economic games, together with behavioral analyses and computational reinforcement learning modeling. Our cross-sectional sample spanned from late childhood into early adulthood (8 to 23 years old, *N*=244). Participants played age-appropriate versions of two well-studied incentivized economic games: A Trust Game (Figure 1B) and a Coordination Game (Figure 1D). These two games involve key types of cooperative behaviors: trust and coordination. Trust is key for mutually beneficial cooperation to be initiated and sustained (e.g., Berg et al., 1995; van den Bos et al., 2010; van den Bos, van Dijk, et al., 2012), and for achieving beneficial outcomes for all interaction partners involved. Yet, trust also creates a hazard of being betrayed. Similarly, coordinating one's behavior with others is often critical for collective welfare, even though outcomes may not always equally benefit all interaction partners (Luce & Raiffa, 1989; Osborne & Rubinstein, 1994).

The two games consisted of repeated one-shot interactions, in which both players had to choose between two options. In each trial, they encountered one new anonymous player from either a Cooperative environment or an Uncooperative environment in two games (the Trust Game and Coordination Game). The decisions of these players had been recorded in a previous session with age-matched unfamiliar others (see *Methods, pre-test*). Participants were explained that between environments, players could differ in their tendency to choose X (see Figure 1B and 1D). To maximize their earnings, participants had to learn over the course of the game which environment was Cooperative and which environment was Uncooperative, and adjust their choices accordingly. That is, in the Trust Game they had to learn in which environment the typical behavior was choosing X (labelled the 'Trustworthy environment') and in which environment the typical behavior was choosing Y (labelled the 'Untrustworthy environment'). Participants maximized their monetary outcomes by trusting (i.e., choose A) Trustworthy others and withhold trust (i.e., choose B) from Untrustworthy others. Similarly, in the Coordination Game, participants had to learn in which environment players tended to choose X (labelled the 'Friendly environment') and in which environment they tended to choose Y (labelled the 'Unfriendly environment'). Participants maximized their outcomes by coordinating with the response of the others, i.e., participants accepting a disadvantage (i.e., choose A) when interacting with the 'Unfriendly environment', or accepting an advantage (i.e., choose B) when interacting with the 'Friendly environment'. The social environments in these games were probabilistic, as cooperative behaviors were displayed by 73% of the players in the Cooperative environments, and by 27% of the players in the Uncooperative environments.

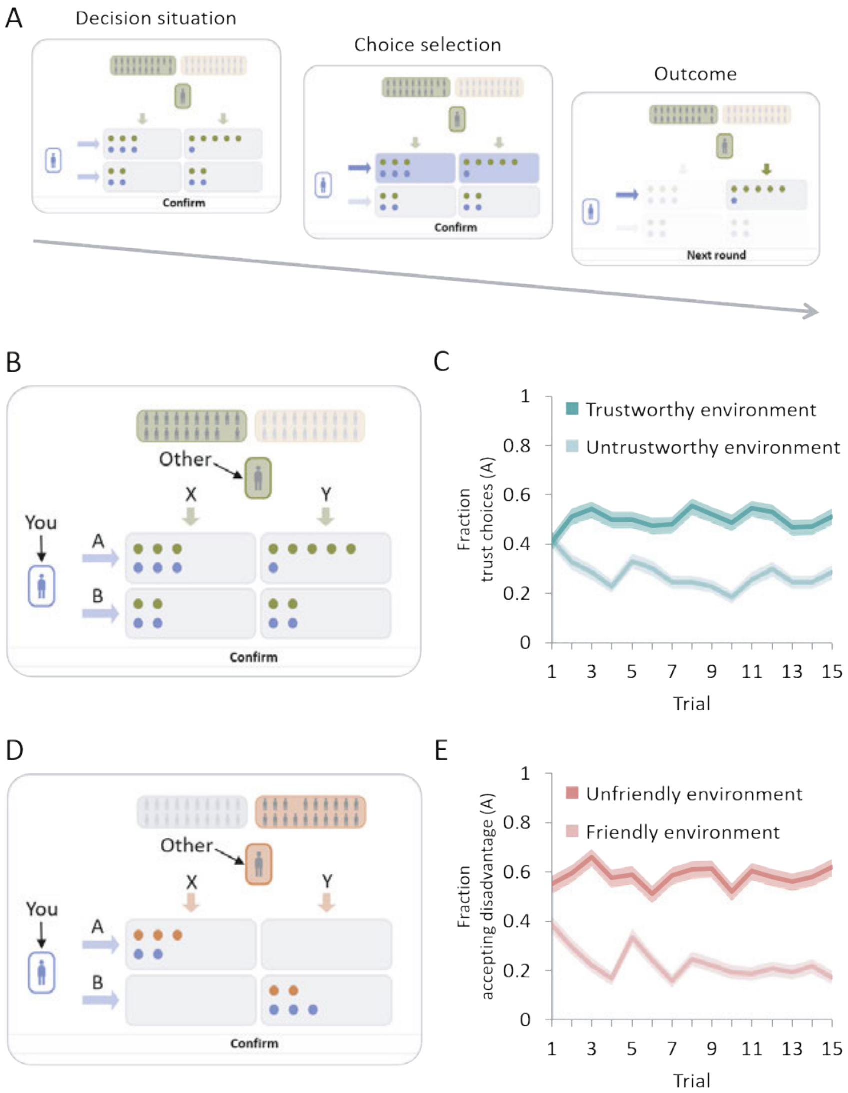


Figure 1. Task assessing learning to adjust to cooperative and uncooperative social environments. **(A)** Example trial. The participant (purple stick figure on the left) can choose between the top and bottom row of boxes (A or B). After choice selection, the participant is shown the pre-recorded choice (X or Y) of the other player (grey stick figure on the top). The background color of the other player indicates to which of the two environments they belong. The combined choices of the participant and the other player determine the monetary outcome for both players (number of dots in their corresponding color). **(B)** In the Trust Game, participants interact with players from a 'Trustworthy' environment (who tend to choose X) or an 'Untrustworthy' environment (who tend to choose Y). Participants' own monetary payoffs are maximized by choosing to trust (choose A) a player from a Trustworthy environment, and to withhold trust (choose B) from a player from the Untrustworthy environment. In this Trust Game

setup only disadvantageous inequality aversion may play a role in decision making. **(C)** Participant choices over trials per social environment, pooled across all participants. Over the course of the game, participants adjusted their choices by directing their trust towards players from the Trustworthy environment, and away from players from the Untrustworthy environment (N=244). **(D)** In the Coordination Game, participants' monetary payoffs are also maximized by matching the choices of their co-players. Again, social environments differ in their prevalence of (non)cooperation, reflected by players' tendencies to choose either X or Y. Coordinating on either of the outcomes (A,X) or (B,Y) will lead to positive outcomes. Respectively, participants' own monetary payoffs are maximized by choosing to accept a disadvantage (choose A) when confronted with a player from the Unfriendly environment, and to accept an advantage (choose B) when confronted with a player from the Friendly environment. In this game both advantageous and disadvantageous inequality aversion may play a role in social decision making. **(E)** Participant choices over trials per social environment, pooled across all participants. Overall, participants learned to coordinate with players from both environments. (N=202). Shaded areas in panels c and e represent standard errors of the mean (s.e.m.).

Participants also played an iterative Ultimatum Game (UG) and Dictator Game (DG), which allowed us to estimate participants' social preferences (i.e., advantageous and disadvantageous inequality aversion; see *Methods*). We separately assessed participants' prior expectations of the behavior of others before the start of the Trust Game and Coordination Game (see *Methods*). Furthermore, we used computational reinforcement-learning models (Daw et al., 2011) to model the updating of expectations between interactions. In these models, the learning rate quantifies how much an expectation violation modifies our subsequent expectations and consequently our decision making. We allowed learning rates to decay over the course of the games because we expected that most of the learning about the environments would happen in the first set of trials. After that, behavior would stabilize, provided the environments did not change their behavior (for more on learning rates and environmental stability see (Behrens et al., 2007; Li et al., 2011; Nassar et al., 2012)). We extended these reinforcement learning models to account for the measured prior expectations and social preferences (van den Bos et al., 2013), and compared the parameters of these models across age cohorts (see *Methods*).

We hypothesized that participants would be able to learn to adjust their behaviors to social environments differing in their level of (non)cooperation, but that across adolescence this ability would improve rapidly. We expected that these developmental differences could be explained by a combination of (1) social preferences (i.e., age-related changes in levels of advantageous and disadvantageous inequality aversion), (2) prior expectations (i.e., age-related changes in expectations about others' trustworthiness and tendencies to prioritize their own payoffs over those of others) and (3) updating of expectations (i.e., age-related changes in learning rates).

Results

Learning to adjust to cooperative and uncooperative social environments across age

First, we examined decisions over the course of the games to assess whether children, adolescents, and young adults adjust their behavior to different social environments with different levels of cooperation. For this, we used the Trust Game in which participants maximized their monetary outcomes by trusting Trustworthy others and withhold trust from Untrustworthy others (Figure 1B), and the Coordination Game in which participants maximized their outcomes by coordinating with the response of the others, i.e., participants accepting an advantage when interacting with the 'Friendly environment', or participants accepting a disadvantage when interacting with the 'Unfriendly environment'. We performed a binomial generalized linear mixed model (GLMM) per game on participants' binary choices, including social preferences and prior expectations of others' behavior (see *Methods*).

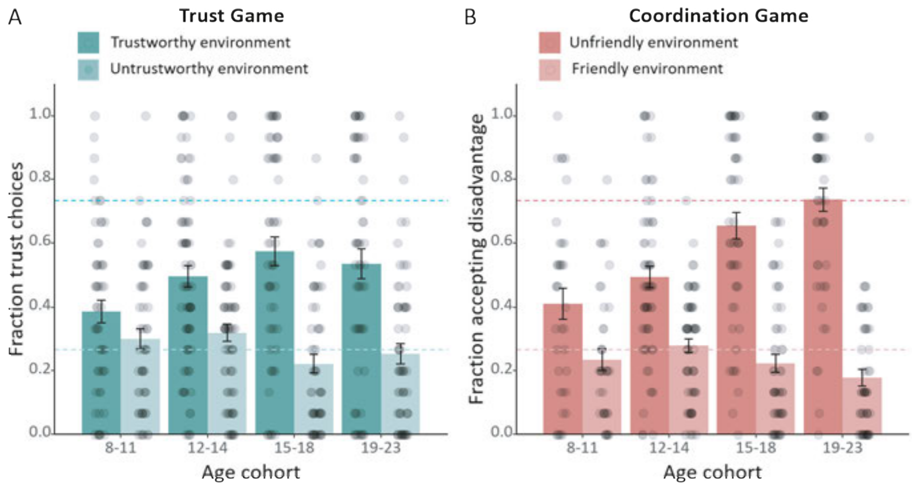


Figure 2. Developmental asymmetries in adjusting to cooperative and uncooperative social environments. Decisions per age cohort are shown per social environment in the **(A)** Trust Game (*N* = 244) and **(B)** Coordination Game (*N* = 202). Across age cohorts, there is a pronounced increase in cooperative choices (i.e., trusting players from a Trustworthy environment in the Trust Game, and accepting a disadvantage from players from an Unfriendly environment in the Coordination Game), whereas uncooperative choices (i.e., withholding trust from players from an Untrustworthy environment in the Trust Game, and accepting an advantage from players from a Friendly environment in the Coordination Game) were relatively stable across age. Dashed lines in a and b indicate the reinforcement rates (i.e., fraction of 0.73 and 0.23) for each social environment. Note that we grouped participants for illustration purposes only and age was treated as a continuous variable in all analyses. Error bars represent s.e.m.

For the Trust Game, results indicated an accelerated change in adolescence in which people differentiated more between the Trustworthy and Untrustworthy environment (environment x age linear, B = -0.307, p < .001; environment x age quadratic, B = 0.205, p = .015; N=244; see Table S1 for full statistical analysis; Figure 2A). Post-hoc tests per social environment showed that trusting the Trustworthy others increased rapidly in early to mid-adolescence (age linear, B = -0.384, p = .006; age quadratic, B = 0.316, p = .020). In contrast, adjusting to Untrustworthy others improved slightly, and monotonically across adolescence (age linear, B = 0.233, p = .031).

For the Coordination Game, results again indicated that with age, people differentiated more between the Friendly and Unfriendly environment (environment x age linear, B = -0.458, p < .001; N = 202; see Table S3 for full statistical analysis; Figure 2B). Post-hoc tests per social environment showed that optimally coordinating to the Unfriendly environment (i.e., participants accepting their disadvantage) increased across adolescence (age linear, B = -0.446, p < .001). However, coordinating to the Friendly environment (i.e., participants accepting their advantage) did not change with age; participants from all age cohorts adjusted quickly to this environment. Together, these results show that people coordinated to both environments but younger participants were less likely to accept a disadvantage than older participants.

Social preferences and prior expectations

Social preferences (advantageous and disadvantageous inequality aversion) and prior expectations of others' behavior are features that may account for age-related changes in learning to adjust to different social environments. Before further testing their relation to behavior in the Trust Game and Coordination Game, we first examined the age-related changes in these parameters. Robust linear regression analyses (5000 bootstraps) indicated that only disadvantageous inequality aversion changed across age (Figure 3A-3D). Specifically, older participants were, compared to younger participants, less averse to being behind (age linear, B = -0.098, β = -0.308, p < .001, 95% CI = [-0.139, -0.057], N = 244). We did not observe significant age-related change for advantageous inequality aversion (age linear, B = -0.099, β = -0.118, p = .133, 95% CI = [-0.229, 0.031], N = 202), nor for prior expectations of others' trustworthiness (age linear, B = -0.048, β = -0.085, p = .209, 95% CI = [-0.124, -0.027], N = 245) or for prior expectations of others' tendency to prefer to have more than the other (age linear B = -0.031, β = -0.076, p = .209, 95% CI = [-0.087, -0.024], N = 245).

In a binomial GLMM analysis, advantageous and disadvantageous inequality aversion were related to choices in the games (see Tables S1 and S3 for full statistical analysis). Greater disadvantageous inequality aversion was associated with overall fewer trusting choices (B = 0.215, p = .012) and with fewer choices in which participants accepted a disadvantage (B = 0.134, p = .048). In addition, greater advantageous inequality aversion was associated with greater acceptance of a disadvantage (B = 0.172, p = .009). In contrast, prior expectations were not related to choices in both games.

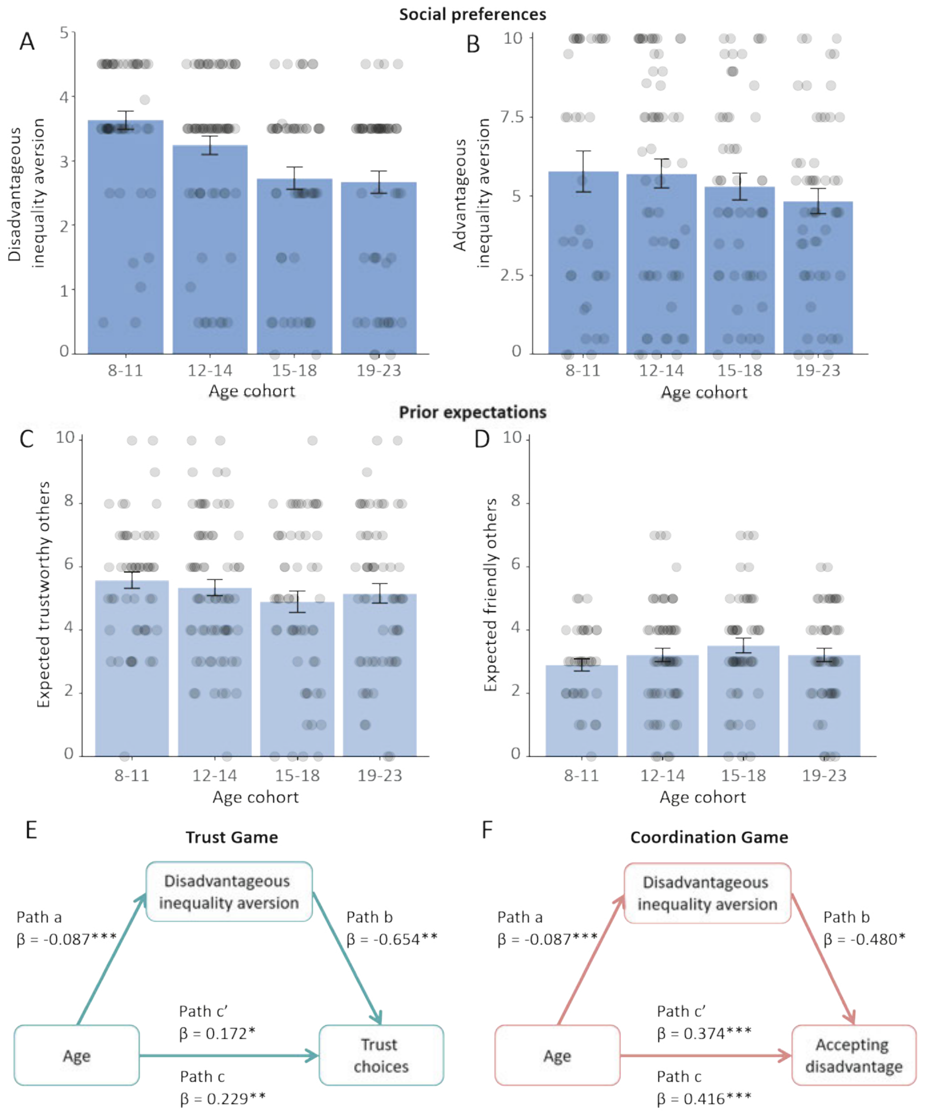


Figure 3. Social preferences and prior expectations across age cohorts. Social preferences and prior expectations are features that may account for choices in the games. **(A)** Indifference points of the Ultimatum Game as a measure of disadvantageous inequality aversion and **(B)** Indifference points of the Dictator Game as a measure of advantageous inequality aversion were used as social preference measures. **(C)** Prior expectations for the Trust Game, with higher values indicating greater expectations

that others are Trustworthy. **(D)** Prior expectations for the Coordination Game, with higher values indicating greater expectations that the others are Friendly (i.e., not tending to prioritize their own payoffs over those of others). In panels a-d, error bars show s.e.m. **(E)** Mediation model for the effect of age on trust behavior towards players from the Trustworthy environment (controlled for trust choices towards players of the Untrustworthy environment), via disadvantageous inequality aversion. **(F)** Mediation model for the effect of age on coordination behavior (i.e., accepting a disadvantage) when confronted with players from the Unfriendly environment (controlled for accepting disadvantages when playing with the Friendly environment), via disadvantageous inequality aversion. Note in mediation models: c = total effect, c' = direct effect; values are standardized regression coefficients of direct effects, and asterisks indicate significance levels (**p* < .05, ** *p* < .01, *** *p* < .001).

To better understand what drives the age-related change in learning to adjust to the social environments differing in their level of cooperation, we ran a mediation analysis per game. Specifically, we examined whether the age-related changes the observed increase in cooperative behavior (trusting, accepting a disadvantage) across development, was explained by the age-related change in disadvantageous inequality aversion (Figure 3E; Figure 3F). We found that, when controlled for choice participants' choice behavior in the Untrustworthy environment, the improvement across age in adjusting to the Trustworthy environment ($\beta = 0.172$, $p = .026$) was partly explained by the age-related decrease in disadvantageous inequality aversion (indirect effect = 0.057, *SE* = 0.026, 95%CI = [0.011, 0.113]). That is, older participants showed lower levels of disadvantageous inequality aversion ($\beta = -0.087$, $p < .001$), which in turn resulted in more trust choices ($\beta = -0.654$, $p = .007$; Figure 3E). This mediation analysis for the Coordination Game similarly showed that, when controlled for choice behavior in the Friendly environment, the age-related improvement in coordinating with the Unfriendly environment ($\beta = 0.374$, $p < .001$) was partly explained by disadvantageous inequality aversion (indirect effect = 0.042, *SE* = 0.020, 95% CI = [0.005, 0.083]). That is, older participants showed lower levels of disadvantageous inequality aversion ($\beta = -0.087$, $p < .001$), which in turn resulted in more acceptance of a disadvantage when coordinating with the Unfriendly environment ($\beta = -0.480$, $p = .022$; Figure 3F). Note that this partial mediation in the Coordination Game did not hold when advantageous inequality aversion was included as an additional mediator.

Computational modeling of updating expectations

To understand how children, adolescents, and young adults update their expectations in different social environments, we developed computational models that extend basic reinforcement learning models(Rescorla & Wagner, 1972). In our models, participants use the outcome of interactions to update their expectations of their interaction partners' choices in each social environment (Figure 4A-C). The extent to which these expectations are updated is reflected in a learning rate (λ). Besides quantifying the updating of expectations, this computational approach allows us to confirm the role of social preferences as observed in our behavioral analyses. We extended the basic reinforcement model by i) incorporating mean cohort-level social preferences to calculate a subjective value of interaction monetary outcomes (Figure 4A, 4C) that drives decision making, and ii) by allowing learning rates (expectation updating) to exponentially decay over trials of the game. Thus, we fitted four variants of this model (with and without social preferences; with and without decaying learning rates) to our experimental data for each age cohort and each game, to allow estimating different parameters (learning rates, expectation updating) across cohorts per game (see *Methods*).

For both the Trust Game and the Coordination Game, a comparison of model fits provided strong support for models extended with social preferences (Figure 4D), confirming the results from our behavioral analyses that social preferences impact decision making. The best models also included decaying learning rates (see Figure 4D and Table S7). For the Trust Game, we observe that for the 8-11 year-olds, estimated learning rates are constant over the course of the game, suggesting that in late phases, individuals in this youngest age cohort still updated their expectations of the behavior in the different social environments. In the older age cohorts, learning rates start high (around λ=1; asymptote not shown in Figure 4E) and decay over trials, indicating that expectations take form relatively early in the game, and remain relatively stable later on. For the Coordination Game (Figure 4F), we observe a similar pattern: older participants tended to show the strongest decay in learning rates over trials, whereas participants from the younger cohorts tended to update their expectations throughout the game.

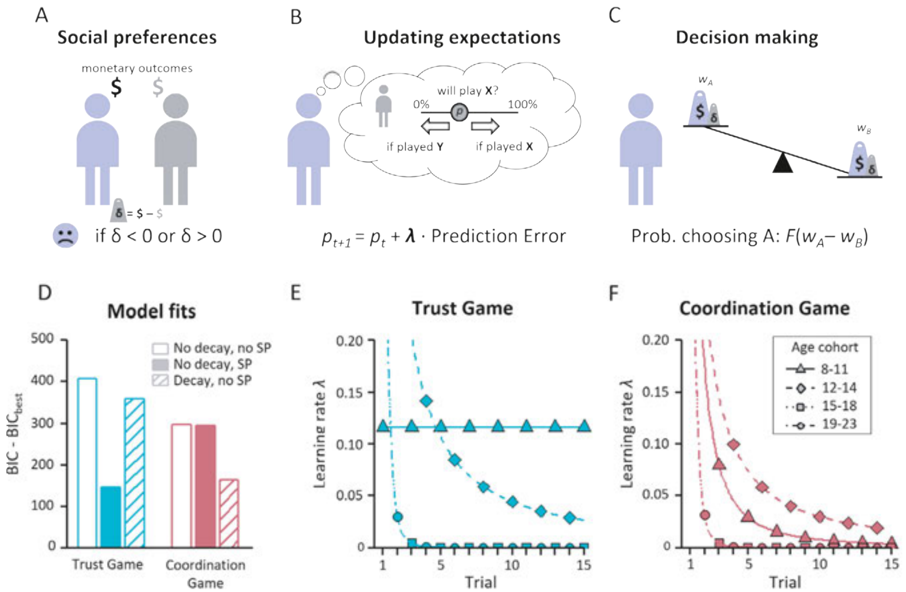


Figure 4. Model of reinforcement learning with social preferences. **(A)** Individuals acquire monetary payoffs ($) from interactions in the games (*cf.* Figure 1). How they subjectively value each outcome can be influenced by their social preferences (Fehr & Schmidt, 1999), whose impact is proportional to the differences in payoff between interaction partners (δ). **(B)** Over the course of the games, individuals update their expectations (*p*) about the behavior of the other players. The extent of updating is proportional to the prediction error (i.e., the difference between the expected and actual outcome) and learning rate *λ* (Sutton & Barto, 1998). **(C)** The probability that an individual chooses A (not B) is an increasing function (*F*) of the difference in weight of the two choice options (w_A and w_B; Methods). We use maximum likelihood methods to estimate learning rates *λ* for each age cohort and each game separately. In the baseline model, the weights reflect individuals' monetary payoff from their interactions ($) and *λ* is constant over trials. Extended models also incorporate social preferences and learning rates that decay exponentially over game trials (see *Methods*). **(D)** For both games, bars show BIC differences of three model variants with the best model, which includes both social preferences (SP) and decaying learning rates. For each model, BIC values were calculated by summing BIC values of all age cohorts. Solid bars reflect models including social preferences; void and hatched bars respectively show models excluding and including decaying learning rates. **(E)** Estimated learning rates from the best models as a function of the trial number, for each of the four age cohorts separately for the Trust Game, and **(F)** for the Coordination Game. For the older cohorts (15-18 and 19-23), the estimated learning parameters were virtually identical, causing the plotted lines to coincide.

Discussion

Here, we examined children's, adolescents' and adults' ability to learn to adjust to social environments that differ in their level of cooperation. We examined the role of social preferences (inequality aversion), prior expectations about others' behavior, and the updating of expectations as potential mechanisms underlying this behavior. To this end, participants played a series of economic games with groups of age-matched unfamiliar others, which captured two important cooperative behaviors: trust and coordination behavior. Our results show a striking developmental asymmetry in the learning to adjust to (un)cooperative environments: people adjust well to environments that require uncooperative behavior (i.e., withholding trust, accepting an advantage) from a young age, yet only during adolescence they learn to adjust to environments that require cooperative behaviors (i.e., trusting, accepting a disadvantage). Our results provide several insights into the mechanisms that explain these age-related differences.

First, age-related differences in learning to adjust to cooperative behaviors can be partly explained by differences in social preferences. Specifically, older participants showed lower levels of disadvantageous inequality aversion which explained their higher levels of cooperative behaviors in a Trust Game and Coordination Game. That is, younger participants are less willing to cooperate (trust, accept a disadvantage) given that they are more averse to potential non-cooperation of the other player. Moreover, our computational models confirmed that participants' decisions were best captured by a reinforcement learning model extended with social preferences in all age bins. Note that in our current RL modeling approach social preferences influence choice behavior through a subjective transformation on the participants' expected payoffs in these games. This way, the RL models show e.g., how disadvantageous inequality aversion (dislike of being behind) can reduce the ability to adjust to environments that require cooperative behaviors. Future work should explore whether other factors underlie the age-related changes in social preferences and their mediating effects on cooperative (adjusting) behaviors. For example, the willingness to punish disadvantageous outcomes, or trying to force the other to coordinate in your favor may be alternative motivations underlying these effects. However, those questions are better answered by using experimental designs in which participants play multiple rounds with the same person, rather than a series of one-shot games. Taken together, our results underline that for understanding age-related changes in social decision making it is critical to understand the development in social preferences, which differ across developmental windows and largely drive social decision making.

A potential mechanism that may relate to the influence of inequality aversion on decision making, is behavioral control (McAuliffe et al., 2017). Behavioral control refers to the ability to control thoughts and actions in order to regulate behavior towards (long-term) goals (Miller & Cohen, 2001; Steinbeis, 2018b). Developmental studies have shown that behavioral control undergoes protracted development due to a prolonged maturation of underlying neural circuitry in regulatory brain regions including the prefrontal cortex (Achterberg et al., 2016; Steinbeis, 2018b; van den Bos et al., 2015). In turn this would result in developmental changes in responses to inequality into childhood and presumably into adolescence (Meuwese et al., 2015; Sul et al., 2017). An experiment in children also confirmed a direct role of behavioral control in behavior that benefits others: taxing children with a response inhibition task resulted in less prosocial behavior and more costly punishment to violations of fairness (Steinbeis, 2018a). An alternative explanation is that inequality may evoke stronger emotional responses, such as increased levels of anger (Güroğlu et al., 2011; van den Bos, van Dijk, et al., 2012). This would yield a different view on social preferences in which responses to inequality can be based on emotion regulation ability. Future studies are necessary to further disentangle whether such self-regulatory behaviors drive the development of social preferences and their influence on cooperative behaviors. Consequently, an interesting field for future studies is whether strengthening self-regulatory processes is a promising pathway for stimulating co-operative behavior in young people.

Besides social preferences, we also examined how people's *prior expectations* of others' trustworthiness and inclination to take more than others influenced learning in different social environments. Our results indicated that reported prior expectations of others' behavior were stable across age cohorts. This is surprising given the consistently reported increase in cooperativeness across age (e.g., Blakemore & Mills, 2014; Eisenberg et al., 1991, 1995; van den Bos et al., 2010), which was also observed in the current experiment. This suggests that there is a developmental mismatch between prior expectations and the actual levels of co-operation. Moreover, contrary to our hypotheses, we did not find effects of prior expectations on learning to adjust to different social environments. Perhaps people do not have strong prior expectations about others' behavior in the anonymous games used in the current study, and any expectations they might have are overridden quickly by outcomes of interactions. Presumably, effects of prior expectations in the current setup would be more prominent in a more heterogeneous sample with greater diversity in - for example - life-history backgrounds. For instance, prior expectations (as well as the updating of these expectations), may be different for people who have grown up in an environment where rewards and punishments are unpredictable, this may be particularly the case for children who have experienced harsh and inconsistent discipline, maltreatment and neglect (Hanson et al., 2017; Pitula et al., 2017). These expectations of others' behavior may match their environmental experiences and as such, they may engage in social situations differently. Thus, when assessing the generalizability of our results it would be important to include a more heterogeneous sample with greater diversity in life-history backgrounds. Including different populations could also help answering the question to what extent prior expectations about behavior in games reflect prior expectations about cooperative behavior in the real world (e.g., Benz & Meier, 2008).

Here we used computational modeling to quantify how quickly children and adolescents updated their expectations based on choice outcomes in previous interactions. Interestingly, when placed in a new social environment, people were initially highly sensitive to behaviors of other players, and quickly adapted their behavior to the outcomes they experienced. For older ages, behavior stabilized after a few interactions as signaled by a decrease in learning rate. Children and young adolescents, however, continued to react to the choices of others across the games. That is, they often switched strategies after a surprising response from one of the environments. This finding indicates that during adolescence, people more effectively integrate outcomes over time, and consequently form stable expectations of others based on their behavior, which are not quickly overridden by a single experience. Building lasting relations may crucially depend on this integrated information of others' behavior. Although the continuous expectation updating of children and adolescents hampers their learning in stable environments, this actually may provide an advantage in fast-changing or unpredictable environments (Nussenbaum & Hartley, 2019). That is, in such environments, immediately responding to changing feedback is more beneficial than sticking to prior expectations (Decker et al., 2015). Whether fast-updating better fits children's and adolescents' experienced social environments is an interesting question for future studies.

In the current study, participants were confronted with choices from actual peers and real-life consequences of their actions for all interaction partners. This two-directional approach, rather than often-used one-way decision making, is acknowledged as an important aspect of paradigms in social sciences (Camerer & Mobbs, 2017). However, the controlled social environments in our study are less complex than real-life social interactions, in which factors such as social status, culture, or reputation may complicate social decision making. Future studies, e.g., field studies or studies using virtual reality, could aim to further approach the complexity of real-life social interactions, while retaining experimental control. In addition, we included a specific experimental set-up of social learning in which participants were given prior information on the different social environments. Future studies will need to assess whether our developmental findings hold in settings where participants need to figure out base rates of cooperativeness and exploitation on their own. Another limitation of the current study is that whereas social preferences were revealed preferences, prior expectations were stated expectations about others. People find it hard to estimate probabilities, and future studies need to assess the validity of these preferences with individual difference measures. Moreover, although IQ did not differ between groups and did not influence any of our findings, our adult participants were mainly recruited through university advertisements. Future studies should aim for a representative sampling strategy in each age cohort. A final limitation of the current study is its cross-sectional design, as longitudinal studies are necessary to identify developmental patterns. Therefore, developmental interpretations of behavioral results and the underlying mechanisms remain speculative.

In sum, we combined computational learning models and experimental social manipulations to demonstrate age-related changes in adjusting cooperative behaviors. Well-developed social skills are essential for succeeding in society and long-term positive outcomes. The ability to adapt to different social environments and discern who we should trust and cooperate with, may benefit short-term outcomes, but may also foster social relationships and restrain behavioral and mental health problems in the long-term (Crone & Dahl, 2012; Dahl et al., 2018; Paus et al., 2008; Sawyer et al., 2018). Knowledge of how such social adjustment behavior manifest in different developmental stages inform what ages are the important developmental phase for monitoring social development, and what ages are potentially more receptive to interventions (Dahl et al., 2018; Yeager et al., 2018).

Our study has shown that adjusting cooperative behaviors is developing rapidly in early adolescence. Improvements in adjustment to different social environments are driven by developing social preferences (waning aversion to disadvantageous inequality aversion) and increasingly effective updating of own behavior in response to others' behavior. Early adolescence would, therefore, be a key target window for interventions targeted at stimulating cooperative and well-adjusted social behavior. Moreover, these findings provide important starting points for interventions for youth with maladaptive social tendencies, such as youth with conduct disorder problems(Frick & Viding, 2009; Viding & McCrory, 2019).

Methods

Participants

A total of 269 participants (58.4% female) between ages 8 and 23 years took part in this study. Participants were recruited from a primary school (*n* = 60), two secondary schools (*n* = 128), and through local advertisements at a university campus (*n* = 81) in the western and middle part of The Netherlands. The majority of the participants (92.3%) were born in the Netherlands, and a minority was born elsewhere (Morocco 1.4%; all other countries <1%), or information was missing (1.4%). Twenty participants from secondary schools (ages 14-16) were excluded due to technical problems with saving the learning data. Four participants were excluded because they did not finish the cognitive behavioral measures, and therefore IQ could not be estimated. The final sample consisted of 245 individuals aged between 8 and 23 years.

Adult participants provided written informed consent. For minors, written informed consent was obtained from parents. To make the tasks incentive-compatible, participants were informed that with each behavioral task they could win points that represented lottery tickets. In each class, and in a similar-size group of adults, one lottery ticket was randomly drawn and the winner received a digital 10 Euro gift voucher. In addition, all minors received a small gift; adults received 10 Euros flat rate or course credit. All procedures were approved by the Psychology Research Ethics Committee of Leiden University (minors: CEP17-0301/120;

young adults: CEP17-1009/334) and performed in accordance with the relevant guidelines and regulations.

For analyses using age cohorts (see *Computational modeling* in the section below), we divided the sample into four roughly equally-sized age cohorts: 8-11 year-olds (n=54, 46.3% female, mean age 10.6, SD 0.9), 12-14 year-olds (n=73, 52.1% female, mean age 13.4, SD 0.7), 15-18 year-olds (n=57, 59.6% female, mean age 17.0, SD 1.3), and 19-23 year-olds (n=61, 80.3% female, mean age 21.1, SD 1.4). A χ^2-test indicated sex differences between age cohorts ($\chi^2_{(3)}$ = 16.6, p = .001), with more females in the oldest age cohort. IQ was estimated using a speeded version of the Raven Standard Progressive Matrices (Hamel & Schmittmann, 2006). The estimated IQ scores were largely within the normal range varying between 79 and 136 (mean IQ = 106, SD = 10.3), and did not differ significantly between age cohorts (F (3,237) = 2.18, p = .090) and sexes (F (1,237) = 0.28, p = .770). Additional analyses showed that sex differences and IQ did not confound performance on the social games, and did not influence any of our observed age-related changes therein (see Tables S2 and S4).

Pre-test

A key component of the economic games used in the current study is that choices have consequences not only for oneself, but also for the other player. To ensure this, we performed a pre-test at a separate high school and a separate adult sample (both in The Netherlands) functioning primarily as a match for determining the participants' outcomes and thereby creating a true social consequence of behavior.

In total, 82 adolescents and 44 adults were asked to make one choice (X or Y) for each social game (Trust Game and Coordination Game, see Figure 1). We randomly linked each participant in the full-experiment with one pre-test participant. This match and the combined outcomes of their choices determined the outcome for the participants (number of points), as well as for the pre-test participant. The pre-test participants had a similar lottery ticket procedure as the participants from the full experiment, i.e., points were lottery tickets with which they had a chance of winning a 10 Euro gift voucher. All pre-test participants received a similar instruction as the participants of the main study. That is, it was stressed that their choices would have consequences for themselves and another participant, since their outcomes would result from their combined choices.

Economic games: Trust Game and Coordination Game

Participants completed two incentivized economic games: A Trust Game and a Coordination Game (Figure 1). Each game was composed of 30 trials in total: each trial was a one-shot game with a new anonymous player (whose decision had been recorded in the pre-test; see above). Every trial the participants chose between 2 options (A or B) to distribute points between themselves and the other. After their decision they could see the choice of the player

(X or Y) and the outcomes for themselves and the player. Outcomes for self and the player resulted from their combined choices, as shown with payoff matrix $\begin{bmatrix} \boldsymbol{a}, a' & \boldsymbol{b}, b' \\ \boldsymbol{c}, c' & \boldsymbol{d}, d' \end{bmatrix}$ where in each of the cells entries with and without apostrophes indicate payoffs for, respectively, the other and self (in bold).

In each of the games, the two social environments consisted of 20 players each (but note that participants interacted with only 15 players per environment). Environments are formed based on pre-test responses, which were matched to create a 'Cooperative' (73%, i.e., 11 out of 15) and an 'Uncooperative' social environment (Figure 1). Over the course of the game trials, participants could learn the tendency of choosing X for each environment of other players, and adjust their responses accordingly. Participants were incentivized by associating their performance to the chance of winning a gift voucher (see Supplementary materials for the instruction protocol).

2

The Trust Game (Figure 1B) was characterized by payoff matrix $\begin{bmatrix} \mathbf{3}, 3 & \mathbf{1}, 5 \\ \mathbf{2}, 2 & \mathbf{2}, 2 \end{bmatrix}$. Participants could maximise their earnings by choosing A ('trust'; top row) when matched with a member of the Trustworthy environment, and choosing B ('not-trust'; bottom row) when matched with a member of the Untrustworthy environment. The Coordination Game (Figure 1D) was characterized by payoff matrix $\begin{bmatrix} \mathbf{2}, 3 & \mathbf{0}, 0 \\ \mathbf{0}, 0 & \mathbf{3}, 2 \end{bmatrix}$. Participants could maximize their earnings by coordinating to their partners' choices. That is, the participant needed to accept a disadvantage (choose A; top row) when matched with a member of the 'Unfriendly' environment, but when matched with a member of the 'Friendly' environment the participant needed to accept an advantage (choose B; bottom row).

The order of these two games was counterbalanced across participants. Within each game, participants played 30 trials, 15 trials with each environment of players (e.g., Trustworthy and Untrustworthy environment). The inconsistent choices within an environment (e.g., Y when playing with someone of the environment that prefers X) were distributed across trials, yet fixed on trials 4, 8, 12, and 14. Within a game, the order of interactions with the two different environments was presented randomly, yet fixed across participants.

Although our main research questions center on the factors specific to learning to adjust behavior in different social environments (e.g., the role of prior expectations about others, and getting more or less than others), we also included a non-social learning task to examine the level of behavioral adjustment in a simple learning context (Figure S1 and Tables S5-S6). In this non-social learning task, participants played with computers as interaction partners, and only the participant – not the computers – could receive payoffs. A formal comparison between age-related changes in learning to adjust to non-social versus social environments is included in the Supplementary materials. A computational modeling approach on the non-social learning task is discussed in Figure S5.

Social preferences

We measured advantageous inequality aversion and disadvantageous inequality aversion in two separate tasks: respectively, a modified Dictator Game (DG) and Ultimatum Game (UG). These measures were derived from an adapted (i.e., child-friendly and short) version of a DG and UG (based on (Beranek et al., 2015; Blanco et al., 2011)). Participants always performed the DG and UG right before the economic games.

In the Dictator Game participants were given six binary choices to divide 10 points between themselves and another anonymous participant in the study; one option was always an unequal distribution (10/0; 10 points for self, 0 points for the recipient) and the other option an equal distribution of points for themselves and the recipient (i.e., starting with (5, 5) and decreasing to (0, 0) with each subsequent trial [(4, 4), (3, 3), (2, 2), (1, 1), (0, 0)] or increasing to (10,10) with each subsequent trial [(6, 6), (7, 7), (8, 8), (9, 9), (10, 10)], depending in the first choice, see Supplementary materials).

In the Ultimatum Game, participants responded to six proposals of another anonymous participant in the study on how to divide 10 points. In the case of a rejection both players earn zero, whereas if the participant accepted the offer, the players get the proposed outcome. The first proposal was an equal split but every next proposal was more beneficial for the other than for self (i.e., (5, 5), (4, 6), (3, 7), (2, 8), (1, 9), (0, 10). For both games, we were interested in the point at which a participant switched their preference from an equal to unequal distribution, or vice versa. This allowed us to infer the point at which participants were indifferent between either distribution. This 'indifference point' represents participants' inequality aversion. That is, higher indifference points in the UG indicate stronger disadvantageous inequality aversion [range 0 - 5], whereas lower indifference points in the DG indicate stronger advantageous inequality aversion [range 0 - 10]. We used indifference points as measures of inequality aversion in all behavioral analyses.

Note that for using social preferences in the reinforcement learning models we transformed the indifference points to measures of advantageous (β) and disadvantageous (α) inequality aversion, following the equations of (Blanco et al., 2011). Accordingly, α varied between 0 - 4.5 and β varied between 0 - 1 (see Supplementary materials for a detailed description, and Figure S4). Note that these transformations are only relevant for the computational modeling as they are used for obtaining a subjective payoff matrix. However, if we rerun the behavioral analyses with these transformed inequality aversions all conclusions remain the same.

Finally, indifference points and inequality parameters α and β can only be calculated for people that show consistency in choice behavior in the DG and UG. In total, 54 participants were excluded due to missing values for social preferences (missing disadvantageous inequality aversion, $n = 1$; missing advantageous inequality aversion, $n = 53$). See Supplementary materials, and Figures S2-S4 for a more detailed description of the Dictator game and Ultimatum Game, and calculation of indifference points and inequality aversion measures (α, β).

Prior expectations

Before the start of each of the economic games (Trust Game and Coordination Game), we assessed participants' prior expectations about the behavior of other people. We asked participants "Suppose that there are 10 other players, how many of these 10 do you think will choose X?" (i.e., 'trustworthy' choice in the Trust Game, or choice to have an advantage over another person in the Coordination Game). This resulted in a prior expectation of the trustworthiness of others (Figure 3C) and a prior expectation of others' tendencies to accept an advantage (Figure 3D), both varying from 0 to 10.

Procedure

All tests were administered in school settings. In the instruction of each learning task, three control questions were included to ensure understanding of the experimental procedure. Two questions quizzed the participant on their understanding of the point distribution (e.g., type how many points each player was winning in a certain choice combination), and one question referred to the color denotation of the two environments. If participants failed one of the control questions, the instruction was repeated until participants understood the procedure of the game. For participants younger than 12, instructions were read out load by an experimenter. All participants completed the tasks by themselves on computers in a quiet environment at school or at the university. Background variables such as the Raven SPM (estimated IQ) and several questionnaires (not relevant to the current study) were administered online using Qualtrics (www.qualtrics.com). In a separate session the DG, UG, and learning tasks were completed using the online software LIONESS Lab (Giamattei et al., 2020).

Statistical analyses of behavioral data

To assess age-related changes in prior expectations and social preferences we ran separate robust linear regression analyses (5000 bootstraps), each with age linear and age quadratic as predictors. Multiple mediation analyses were conducted in SPSS using the computational tool PROCESS version 3.3(Hayes, 2017). For indirect effects, 95% (two-tailed) bias-corrected bootstrapped confidence intervals were calculated using 5000 repetitions. An indirect effect is significant if the confidence interval for the indirect effect does not include zero. These analyses were conducted in SPSS 25, and all tests were two-sided.

Generalized linear mixed models

To analyze choice behavior in the Trust Game and Coordination Game, we fitted logistic generalized linear mixed models (GLMMs) to decisions to choose A (coded as 0) or B (coded as 1) to each game separately. Analyses were conducted in R 3.6.1 (R Core Team, 2020), using the lme4 package (Bates et al., 2014). In all models, participant ID entered the regression as a random intercept to handle the repeated nature of the data. Where appropriate, environment was entered as a random slope in our analyses to handle the differences between individuals in their responsiveness to learning to different levels of (non)cooperation. Our GLMMs included a main effect of environment (e.g., Trustworthy environment, Untrustworthy environment), age in years (linear and quadratic), prior expectations of others' choices and social preferences, and all two-way interactions with environment (see Tables S1-S4 for all GLMM results). Note that for the Trust Game we only added disadvantageous inequality aversion, whereas for the Coordination Game both social preferences were included. That is, in the Coordination Game both types of inequality can occur and drive choice behavior, in contrast to the Trust Game in which only disadvantageous inequality is present.

In all GLMMs, age, prior expectations, disadvantageous and advantageous inequality aversion (mean-centered and scaled) and categorical predictor variables were specified by a sum-to-zero contrast (e.g., sex: -1 = boy, 1 = girl). For the mixed-effects model analyses the optimizer "bobyqa" (Powell, 2009) was used, with a maximum number of 1×10^5 iterations. P-values for all individual terms were determined by Loglikelihood Ratio Tests as implemented in the mixed function in the afex package (Singmann et al., 2020). All statistics, including odds ratios and confidence intervals, are reported in Tables S1 –S6.

Computational modeling

To gain a mechanistic understanding of participants' learning to adjust in the Trust Game and the Coordination Game, we used a basic reinforcement learning (RL) model(Sutton & Barto, 1998) and extended it to accommodate social preferences(Fehr & Schmidt, 1999) (aversion to unequal outcomes). All our models follow the basic logic of RL, in which agents learn about others behavior by updating their expectations with experience. In the case of the games, these expectations (denoted p) concern the behavior of their interaction partners (X or Y; cf. Figure 1). In each trial, p is updated with a magnitude proportional to the prediction error (PE; the difference between the actual and expected choice) and the learning rate λ. Formally, $p_{t+1} = p_t + \lambda \bullet PE$, where $PE = p$ − choice of other (1 if X, 0 otherwise). We fit a set of reinforcement learning models to the data to investigate how λ changes across age cohorts. This parameter is bounded between 0 (which means no updating of expectations at all) and 1 (which means that expectations match the decision of the most recent player).

In our models, the value of p determines the relative weights of w_A and w_B (Figure 4). Each of the games is characterized by a payoff matrix (Figure 1). In each trial t, expected monetary payoffs of choosing A or B are respectively given by $w_{A,t} = p_t \bullet a + (1 - p_t) \bullet b$ and $w_{B,t} = p_t \bullet c + (1 - p_t) \bullet d$. We set the initial value of p_0 to the cohort mean prior measured in our experiment. The probability that a participant chooses A is determined by a standard softmax function:

$\Pr(A) = [1 + e^{-\theta \cdot (w_A - w_B)}]^{-1}$ As there are only two options (A and B) to choose from, the probability of choosing B is simply $1 - \Pr(A)$. In the softmax formula, θ reflects 'decision sensitivity' and accounts for stochasticity in participants' choices: low values of θ indicate high levels of stochasticity ($\Pr(A)$ and $\Pr(B)$ tend to be near 0.5), and high values of θ indicate low levels of stochasticity. In our model fits, θ is a free parameter allowed to vary between 0 and 5.

We extended this baseline model with two factors. First, we include the cohort mean measures of social preferences; that is, we add the measured cohort averages of *disadvantageous* and *advantageous inequality aversion* to calculate w_A and w_B. In particular, for the Trust Game, the weight of option A was penalized with a value proportional to the disadvantageous inequality aversion (i.e., α; note that we drop the subscripts as we assume social preferences to be parameters with a constant value (Fehr & Schmidt, 1999): $w_A = p \cdot a + (1 - p_t) \cdot [\, b - \alpha \cdot (b' - b)\,]$. As for option B the payoffs for both partners are always equal, w_B is unaffected by social preferences. For the Coordination Game, social preferences can affect the weights of both A and B: $w_A = p \cdot \alpha \cdot (a' - a)$, and $w_B = p \cdot \beta \cdot (d - d')$, where β denotes advantageous inequality aversion.

Second, we allowed the learning rate λ to decay over the course of interactions. We implemented this by defining $\lambda_t = \lambda_0 \cdot r^{-\tau}$, where r denotes the trial number, and τ is a free parameter that reflects the speed of the decay in learning, allowed to vary between 0 and 5. The values of the estimated parameters (θ, λ, τ) per age cohort and per game can be found in Table S7. For each of the four age cohorts, we pooled the data and fitted the model with each possible combination of the factors 'social preferences' and 'decay', yielding a total of four models per cohort per game. Note that we also evaluated a potential role for prior expectations by including mean cohort-level prior expectations in the initial valuation of the choice options. However, because prior expectations were relatively close to 5 (range 0 – 10; Figure 2) this was close to the default expectation p of 0.5, marking indifference between the environments at the first choice. Hence, we did not apply formal tests of improved model fit for prior expectations.

Figure 4D shows the goodness-of-fit for each model summed across the four age cohorts relative to the best model, which includes both social preferences and decay. We included a simulation study with a parameter recovery component in the Supplementary materials. Our approach of fitting reinforcement learning models to cohort-level data was motivated by the fact that we had a limited number of observations to accurately fit our model to individual-level choice data. Note that sensitivity analyses with individually-derived parameters indicated this did not influence any of our model-fit conclusions or main findings.

Data and code availability

The data that support the findings of this study, and all relevant R codes can be found on OSF (https://osf.io/z84g6/) and in the Leiden Repository (https://doi.org/10.34894/Z1OYYA).

Supplementary materials

Prior expectations and social preferences: IQ, and sex effects

In a series of robust regression analyses (5000 bootstraps) we examined the effect of IQ and sex effects on participants' social preferences (indifference points) and prior expectations across all ages. We found that estimated IQ was not related to advantageous inequality aversion, prior expectations of others' trustworthiness, and prior expectations of others' tendency to choose more for oneself (all *P*s > 0.1). However, participants with higher IQ were less disadvantageous inequality averse (IQ, B = -0.038, β = -0.308, $p < .001$, 95% CI [-0.053, -0.023]). Also, compared to boys, girls scored higher on advantageous inequality aversion (Sex, B = -1.650, β = 0.245, $p = .001$, 95% CI [-2.569, -0.730]). Compared to boys, girls also expected that others would choose to have more than the participant (Sex, B = 0.457, β = 0.135, $p = .035$, 95% CI [0.033 - 0.881]). We observed no sex differences in disadvantageous inequality aversion and prior expectations of others' trust behavior (all *p*s > .05).

Next, we assessed correlations between advantageous and disadvantageous inequality aversion, and between the prior expectations of the Trust Game and Coordination Game. Inequality aversions were slightly correlated, indicating that people who disliked being behind also liked being ahead ($r = 0.176$, $p = .012$; $N = 202$). This relation was significant even when controlled for age ($r = 0.151$, $p = .032$). Prior expectations about others in the Trust Game and the Coordination Game were not correlated ($r = 0.069$, $p = .282$; $N = 245$), neither when controlled for age ($r = 0.067$, $p = .297$).

Developmental changes in the non-social learning task

To assess whether people are able to adjust their decision-making in a non-social context, we included a non-social learning task with two environments of computer opponents (payoff matrix $\begin{bmatrix} \mathbf{3} & \mathbf{0} \\ \mathbf{0} & \mathbf{3} \end{bmatrix}$, see Figure S1A). Similar to the economic games, participants could maximize their payoffs by coordinating their choices to the choices of the computer opponent. That is, choosing option A when playing against the environment that most often (11/15 trials) chooses X, and choosing option B when playing against the environment that most often (11/15 trials) chooses Y.

We fitted a logistic GLMM to decisions (coded as correct/incorrect) in the non-social learning task, with age linear and age quadratic as predictors. Performance increased linearly with age (Figure S1B; see Table S5 for all statistics).

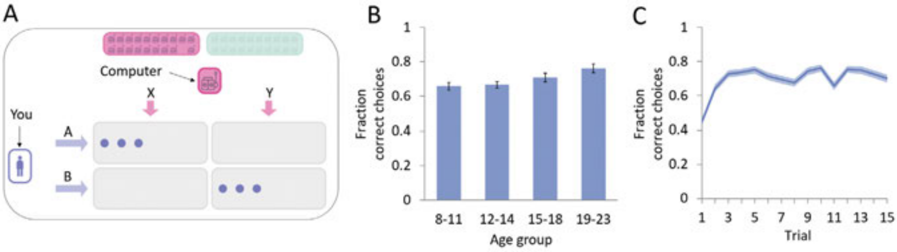


Figure S1. Non-social learning task. **(A)** layout of the learning task. **(B)** performance per age cohort. **(C)** performance over trials pooled across all participants (N=245). Error bars in panel b and shaded areas in panel c show standard error of the mean (s.e.m).

Age-related differences in the non-social vs. social learning game

The main focus of this study was to compare the influence of prior beliefs, social preferences, and feedback-based updating across age groups in different social learning environments. However, the inclusion of a non-social task lends itself for the opportunity to compare learning performance in a social and non-social task more generally. Exploratively, we therefore compared performance in the non-social learning task versus the Trust Game and the non-social task versus the Coordination Game.

We fitted a binomial GLMM to decisions (coded as correct/incorrect) with age linear * type of task (social vs non-social) as predictors. Participant was included as a random intercept to account for the repeated nature of the choice data. Overall performance (grouped across environments) was lower in the Trust Game compared to the non-social learning task; main effect Task p <0.001; Trust Game *Mean* accuracy = 0.613 (*SD* = 0.487); Non-social *Mean* accuracy = 0.699 (*SD* = 0.459). Follow-up tests, showed that this advantage for learning in the non-social task was present for each age group (8-11 years p <0.001; 12-14 years p <0.001; 15-18 years p = .024; 19-23 years p <0.001). A similar GLMM showed that overall performance (grouped across environments) was also lower in the Coordination Game compared to the non-social task; main effect Task p <0.001; Coordination Game *Mean* accuracy = 0.668 (*SD* = 0.470). Follow-up tests showed that this was, however, only the case for the two youngest age groups, and from approximately age 15 adolescents performed -on average- equally well in both games (8-11 years, p < .001; 12-14 years, p < .001; 15-18 years, p = .870; 19-23 years, p = .830). These comparisons between games confirm that specifically young adolescents find it difficult to adjust behavior in social compared to non-social games. Our analyses described in the main paper shed light on what factors underlie age-related change in learning in social environments that differ in their level of cooperation.

Testing confounding effects of sex and IQ on choice behavior in the social-learning games

To assess possible effects of sex and IQ on choice behavior in the learning tasks, we ran additional GLMMs (one per game) that included all predictor variables from the main model (see *General linear mixed-effects models* in main text), and added main effects of sex and estimated IQ. In the Trust Game there were no main effects of sex or IQ (see SI table 2 for all statistics); all effects remained significant after adding sex and IQ to the model – except for the main effect of disadvantageous inequality aversion. In the Coordination Game, there were also no main effects of sex and IQ (see SI table 4 for all statistics). All effects remained significant after adding sex and IQ to the model. In the Non-social learning task, there was no main effect of sex (see SI table 6 for all statistics). However, there was a main effect of IQ ($p < .001$) indicating that participants with a higher IQ had better performance in the non-social learning task. These results suggest that IQ and sex differences did not influence performance on the social learning tasks, and did not influence any of the observed age-related changes in adjustment behavior. However, IQ did relate positively to a general learning tendency in the non-social learning task.

Calculation of social preferences Dictator Game

The Dictator Game (DG) was used to estimate people's advantageous inequality aversion. The aim of the DG is to identify the point at which a participant is indifferent between (10, 0) and the equal distribution. To this end, we always had participants initially chose in the first trial between (10, 0) and (5, 5). The number of points in the subsequent trials depended on the choice in that first trial. That is, if in the first trial a participant selected the equal distribution (5, 5) rather than the (10, 0), the number of points in the equal distribution decreased with one point in each subsequent trial (i.e., (5, 5); (4, 4); (3, 3); (2, 2); (1, 1); (0, 0)). In contrast, if in the first trial the participant selected the unequal distribution (10, 0) over the equal distribution (5, 5), in the subsequent trials the number of points in the equal distribution increased to (10, 10) (i.e., (5, 5); (6, 6); (7, 7); (8, 8); (9, 9); (10, 10)). A participant's inequality aversion is determined by the equal distribution (x, x) which he/she regards as good as the (unequal) distribution (10, 0). For participants with consistent preferences (YY%), this 'indifference point' (*IP*) follows from the point at which they switch from choosing the equal distribution over the unequal distribution (or vice versa; (Blanco et al., 2011). For example, if a participant prefers (10, 0) over (6, 6), but prefers (7, 7) over (10, 0), we assume that *IP* = 6.5.

For participants who switched multiple times from equal to unequal distribution (i.e., who did not show a consistent choice pattern), we fitted a softmax function (see below) to their DG choices to approximate their indifference point. In particular, we coded a choice for the unequal distribution as 0 and the equal distribution (*x*, *x*) as 1. To these choices, 6 for each participant, we then fitted a softmax function $y = [1+\exp(-Z)]^{-1}$, where $Z = a + b*x$.

Subsequently, we solved for y = 0.5 (i.e., -*a* / *b*) if the fitted value of *b* was positive (i.e., when participants tended to choose equal outcomes more often when the value of *x* increased). If the approximated indifference point was outside of the theoretically possible range of [0, 10], we assumed it was undefined. This procedure resulted in approximated switch points *IP'*.

In the Dictator Game, 148 participants showed a consistent choice pattern (i.e., up to 1 switching point, 60%). For 54 participants with multiple switching points we successfully used the softmax function to approximate their indifference point. For 43 participants the approximated indifference point was outside of the theoretically possible range [0, 10], or had a negative values of *b*. These participants where therefore excluded from analyses that used the advantageous inequality aversion measure.

These calculated IP and estimated IP' were used in our behavioral analyses. To include social preferences in subsequent reinforcement learning models we transformed individuals' IPs following Blanco et al. (2011) as: $\beta = 1 - IP/10$. We used the general constraints as formalized by Fehr & Schmidt (1999), with the range of advantageous inequality aversion values limited between 0 and 1. We used these transformed inequality aversions (α and β) to calculate the subjective pay-off matrix in our RL modeling (see *Methods, section Computational modeling* in the main text).

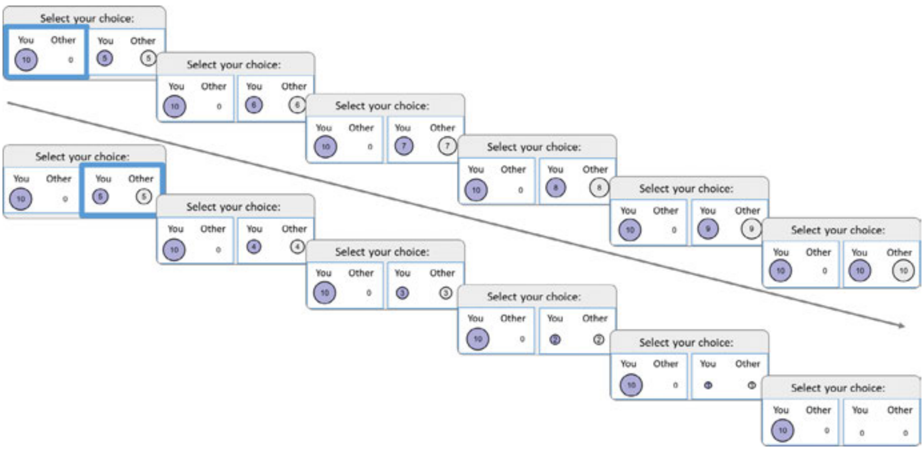


Figure S2. Display of the Dictator Game trials. Trial sequence depends on the choice in the first trial: upper sequence when first choice is for the unequal distribution, lower sequence when first choice is for the unequal distribution.

Calculation of social preferences Ultimatum Game

The Ultimatum Game (UG) was used to estimate people's disadvantageous inequality aversion. The UG is a sequential two-stage game, in which a proposal for a division of points is offered by the proposer, and can be rejected or accepted by the responder. In the case of a rejection both players earn zero. If the responder accepts, players get the outcome proposed. In the proposer stage participants were presented with 10 points and could make an offer to the responder keeping 0 up to 10 points for themselves (i.e., 10 (self), 0 (other); (10, 0); (9, 1); (8, 2); (7, 3); (6, 4); (5, 5); (4, 6); (3, 7); (2, 8); (1, 0)).

In the responder stage, participants were told they were now paired with a new player and that they could accept or reject their proposals (Figure S3). As a responder, participants responded to 6 proposals. The first proposal was an equal split but every next proposal was more beneficial for the other than for self (i.e., (5, 5), (4, 6), (3, 7), (2, 8), (1, 9), (0, 10)). This responder stage was used to obtain a measure of disadvantageous inequality aversion, given that the minimum-acceptable offers in the UG is used as a point estimate of disadvantageous inequality aversion for each individual.

In the Ultimatum Game, the majority of participants showed a consistent choice pattern (i.e., up to 1 switching point, n = 234, 95.5%). In total, 11 participants had multiple switching points (up to 3), and again we used the softmax function described above for the Dictator Game to approximate their indifference point. For 1 participant the approximated indifference point was outside of the theoretically possible range [0, 5]. This participant was therefore excluded from analyses that used the disadvantageous inequality aversion measure.

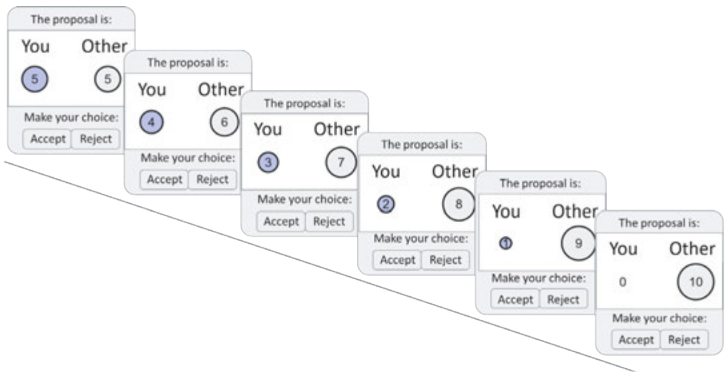


Figure S3. Display of the Ultimatum Game trials (responder stage).

Like in the DG, we used the calculated IPs and estimated IPs in our behavioral analyses. To include individuals' disadvantageous inequality aversion in subsequent reinforcement learning models, we transformed the IPs from the UG following Blanco et al. (2011): $\alpha = IP/(2*(5-IP)$. If there was no rejected offer, we set disadvantageous inequality aversion to 0. If all offers were rejected, disadvantageous inequality aversion was set to 4.5. We used these transformed inequality aversions (α and β) to calculate the subjective pay-off matrix in our RL modeling (see *Methods, section Computational modeling* in the main text).

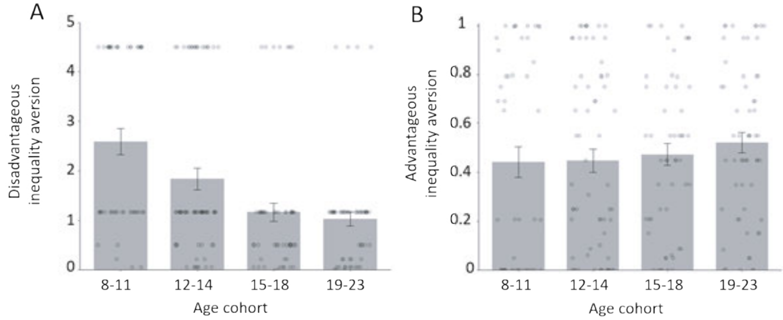


Figure S4. Transformed inequality aversions (α and β) per age cohort. **(A)** Transformed disadvantageous inequality aversion (α), and **(B)** transformed advantageous inequality aversion (β) which are used in the computational RL models.

2

Computational models assessing behavioral adjustment in the non-social learning task

To assess behavioral adjustment outside of social interactions, we fitted the reinforcement models to decisions in the non-social setting (see Figure S5). Following the main text, we pool all data from participants per cohort and consider models with and without decay in learning rates across trials. As there are no other people involved, we do not consider models with or without social preferences, and assume that participants' priors in the first trial are such that they expect their computerized opponent to choose either action with equal (50%) probability.

We observe that models including a decay in learning rates lead to an improved fit. Figure S5 illustrates the estimated learning parameters of the best-fitting model. We observe that for each age cohort, learning rates decreased strongly over time. Interestingly, and in contrast to the Trust Game and the Coordination Game, the least strong decay was observed for the oldest age cohort.

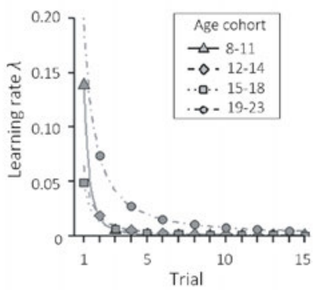


Figure S5. Estimated learning rates per age cohort from the best models for the Non-Social learning task. Best models include decaying learning rates. Estimates learning rates as a function of the trial number, for each of the four age cohorts separately for the Non-Social learning task.

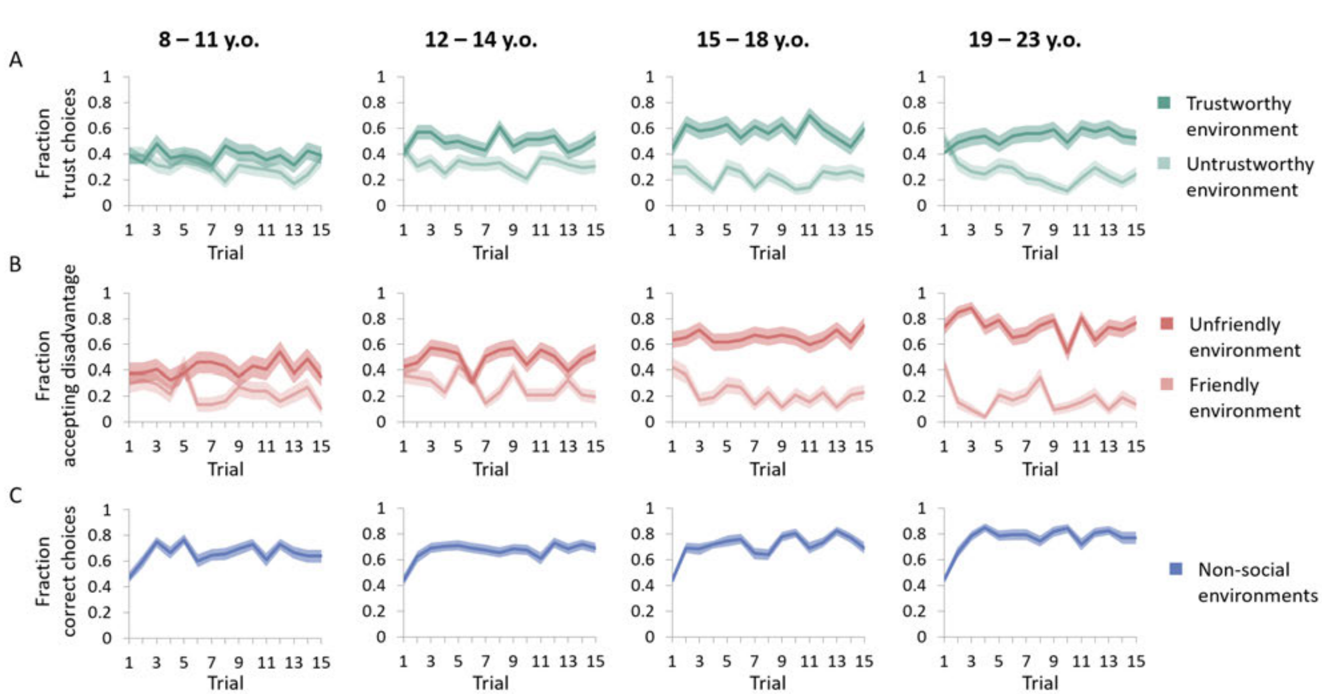


Figure S6. Display of choice behavior over trials per game, separately for each age cohort. Display of choice behavior over trials separately for each age cohort, in **(A)** the Trust Game (N = 244), **(B)** the Coordination Game (N = 202), and **(C)** the Non-social learning task (N = 245). Shaded areas represent s.e.m

Recovery of computational models

To assess the robustness of the computational models presented in the main text, we performed a recovery analysis. For each of the social games (Trust Game and Coordination Game), and for each of the age cohorts separately, we used the parameters of the best fitting models (which included social preferences and a decaying learning rate) to simulate 100 mock data sets. The distribution of mock participants across cohorts was the same as in our behavioral data set. Subsequently, we fitted each of the four models (including and excluding social preferences and decaying learning rates) to the simulated data and compared their fits. This allowed us to examine the recoverability of our models. For both economic games, for each of the 100 simulated mock data sets, the model including social preferences and decaying learning rates fitted the data best, showing that our best fitting model is recoverable.

2

Supplementary Table 1. Mixed-effects model for the Trust Game (N=244) Results of the binomial generalized linear mixed model (GLMM) testing effects of age (linear and quadratic), prior expectations, and disadvantageous inequality aversion (IA), and all 2-way interactions with environment on choice behavior in the Trust Game. Significant effects are in bold. GLMMs are described fully in the main text. Full R-code of this model is: mixed(Choice~cAge-linear*Environment + cAge-quadratic*Environment+ cDisadvantageousIA*Environment + cpriorTrustGame*Environment + (Environment | Subject), method="LRT", family=binomial, data = dat, na.action=na.exclude, control=glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 100000)))

	Estimate	*SE*	χ^2	*P*	*Odds Ratio*	*CI*
Environment	-0,658	0,079	60,751	**<0.001**	0.52	0.44 – 0.60
Age linear	-0,076	0,090	0,700	0.398	0.93	0.78 – 1.11
Age quadratic	0,112	0,087	1,633	0.198	1.12	0.94 – 1.33
Disadvantageous IA	0,215	0,086	6,102	**0.012**	1.24	1.05 – 1.47
Prior expectations	-0,164	0,083	3,827	**0.048**	0.85	0.72 – 1.00
Environment * Age linear	-0,307	0,087	12,203	**<0.001**	0.74	0.62 – 0.87
Environment * Age quadratic	0,205	0,084	5,812	**0.015**	1.23	1.04 – 1.45
Environment * Disadvantageous IA	0,148	0,083	3,139	0.073	1.16	0.99 – 1.36
Environment * Prior expectations	0,106	0,080	1,744	0.183	1.11	0.95 – 1.30
Post-hoc | *Trustworthy environment*						
Age linear	-0,384	0,140	7,324	**0.006**	0.68	0.52 – 0.90
Age quadratic	0,316	0,136	5,330	**0.020**	1.37	1.05 – 1.79
Disadvantageous IA	0,362	0,134	7,182	**0.007**	1.44	1.11 – 1.87
Prior expectations	-0,057	0,128	0,197	0.655	0.94	0.73 – 1.21

Supplementary Table 1. *Continued*

	Estimate	*SE*	χ^2	*P*	*Odds Ratio*	*CI*
Post-hoc | *Untrustworthy environment*						
Age linear	0,233	0,108	4,618	**0.031**	1.26	1.02 – 1.56
Age quadratic	-0,093	0,104	0,785	0.372	0.91	0.74 – 1.12
Disadvantageous IA	0,068	0,103	0,428	0.510	1.07	0.88 – 1.31
Prior expectations	-0,270	0,101	7,125	**0.007**	0.76	0.63 – 0.93

Supplementary Table 2. Mixed-effects model with IQ and sex effects for the Trust Game (N=244) Results of the binomial generalized linear mixed model (GLMM) testing confounding effects of IQ and sex on choice behavior in the Trust Game. Predictors of interest are underlined. GLMMs are described fully in the main text. Full R-code of this model is: mixed(Choice~IQ + sex + cAge-linear*Environment + cAge-quadratic*Environment+ cDisadvantageousIA*Environment + cpriorTrustGame*Environment + (Environment | Subject), method="LRT", family=binomial, data = dat, na.action=na.exclude, control=glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 100000)))

	Estimate	*SE*	χ^2	*P*	*Odds Ratio*	*CI*
<u>Sex</u>	0.047	0.084	0.316	0.574	1.05	0.89 – 1.24
<u>IQ</u>	0.107	0.087	1.501	0.216	1.11	0.94 – 1.32
Environment	-0.656	0.079	60.201	<0.001	0.52	0.44 – 0.61
Age linear	-0.070	0.093	0.556	0.451	0.93	0.78 – 1.12
Age quadratic	0.102	0.088	1.317	0.248	1.11	0.93 – 1.32
Disadvantageous IA	0.244	0.091	7.103	0.007	1.28	1.07 – 1.52
Prior expectations	-0.156	0.084	3.419	0.062	0.86	0.73 – 1.01
Environment * Age linear	-0.307	0.087	12.189	<0.001	0.74	0.62 – 0.87
Environment * Age quadratic	0.205	0.084	5.806	0.015	1.23	1.04 – 1.45
Environment * Disadvantageous IA	0.149	0.083	3.163	0.072	1.16	0.99 – 1.36
Environment * Prior expectations	0.107	0.080	1.754	0.182	1.11	0.95 – 1.30

Supplementary Table 3. Mixed-effects model for the Coordination Game (N=202) Results of the binomial generalized linear mixed model (GLMM) testing effects of age (linear and quadratic), prior expectations, and disadvantageous inequality aversion (IA), and all 2-way interactions with environment on choice behavior in the Coordination Game. Significant effects are in bold. GLMMs are described fully in the main text. Full R-code of this model is: mixed(Choice~cAge-linear*Environment + cAge-quadratic*Environment+ cDisadvantageousIA*Environment + cAdvantageousIA*Environment + cpriorCoordinationGame*Environment + (Environment | Subject), method="LRT", family=binomial, data = dat, na.action=na.exclude, control=glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 100000)))

	Estimate	*SE*	χ^2	*P*	*Odds Ratio*	*CI*
Environment	-1,041	0,086	115,264	**<0.001**	0.35	0.30 – 0.42
Age linear	-0,239	0,071	11,051	**0.001**	0.79	0.69 – 0.90
Age quadratic	0,124	0,068	3,213	0.070	1.13	0.99 – 1.29
Disadvantageous IA	0,134	0,068	3,821	**0.048**	1.14	1.00 – 1.31
Advantageous IA	0,172	0,066	6,689	**0.009**	1.19	1.04 – 1.35
Prior expectations	0,035	0,065	0,281	0.594	1.04	0.91 – 1.18
Environment * Age linear	-0,458	0,093	23,002	**<0.001**	0.63	0.53 – 0.76
Environment * Age quadratic	0,067	0,090	0,537	0.460	1.07	0.90 – 1.28
Environment * Disadvantageous IA	0,068	0,090	0,570	0.450	1.07	0.90 – 1.28
Environment * Advantageous IA	0,260	0,087	8,746	**0.003**	1.30	1.09 – 1.54
Environment * Prior expectations	0,030	0,086	0,117	0.731	1.03	0.87 – 1.22
Post-hoc | *Friendly environment*						
Age linear	0,209	0,100	4,266	**0.037**	1.23	1.01 – 1.50
Age quadratic	0,058	0,097	0,351	0.551	1.06	0.88 – 1.28
Disadvantageous IA	0,077	0,095	0,637	0.420	1.08	0.90 – 1.30
Advantageous IA	-0,083	0,093	0,787	0.372	0.92	0.77 – 1.10
Prior expectations	0,011	0,092	0,013	0.909	1.01	0.84 – 1.21
Post-hoc | *Unfriendly environment*						
Age linear	-0,695	0,130	26,904	**<0.001**	0.50	0.39 – 0.64
Age quadratic	0,193	0,126	2,308	0.126	1.21	0.95 – 1.55
Disadvantageous IA	0,192	0,126	2,289	0.128	1.21	0.95 – 1.55
Advantageous IA	0,425	0,122	11,718	**<0.001**	1.53	1.20 – 1.94
Prior expectations	0,064	0,121	0,279	0.595	1.07	0.84 – 1.35

Supplementary Table 4. Mixed-effects model with IQ and sex effects for the Coordination Game (N=202) Results of the binomial generalized linear mixed model (GLMM) testing confounding effects of IQ and sex on choice behavior in the Coordination Game. Predictors of interest are underlined. GLMMs are described fully in the main text. Full R-code of this model is: mixed(Choice~IQ + sex + cAge-linear*Environment + cAge-quadratic*Environment+ cDisadvantageousIA*Environment + cAdvantageousIA*Environment + cpriorCoordinationGame*Environment + (Environment | Subject), method="LRT", family=binomial, data = dat, na.action=na.exclude, control=glmerControl(optimizer = "bobyqa", optCtrl = list(maxfun = 100000)))

	Estimate	*SE*	*χ²*	*P*	*Odds Ratio*	*CI*
<u>Sex</u>	-0,012	0,067	0,031	0.860	0.99	0.87 – 1.13
<u>IQ</u>	-0,104	0,068	2,286	0.127	0.90	0.79 – 1.03
Environment	-1,043	0,086	115,527	<0.001	0.35	0.30 – 0.42
Age linear	-0,226	0,071	9,758	0.002	0.80	0.69 – 0.92
Age quadratic	0,132	0,068	3,648	0.054	1.14	1.00 – 1.30
Disadvantageous IA	0,101	0,071	2,015	0.151	1.11	0.96 – 1.27
Advantageous IA	0,175	0,067	6,740	0.008	1.19	1.05 – 1.36
Prior expectations	0,023	0,066	0,126	0.722	1.02	0.90 – 1.16
Environment * Age linear	-0,457	0,093	22,829	<0.001	0.63	0.53 – 0.76
Environment * Age quadratic	0,066	0,090	0,527	0.464	1.07	0.89 – 1.28
Environment * Disadvantageous IA	0,068	0,090	0,581	0.445	1.07	0.90 – 1.28
Environment * Advantageous IA	0,260	0,087	8,737	0.003	1.30	1.09 – 1.54
Environment * Prior expectations	0,030	0,086	0,117	0.731	1.03	0.87 – 1.22

Supplementary Table 5. Mixed-effects model for the Non-social learning task (N=245) Results of the binomial generalized linear mixed model (GLMM) testing effects of age (linear and quadratic) on choice behavior in the Non-social Game. Significant effects are in bold.

	Estimate	*SE*	*χ²*	*P*	*Odds Ratio*	*CI*
Age linear	**0.251**	**0.082**	**9.150**	**0.002**	**1.29**	**1.09-1.51**
Age quadratic	0.143	0.083	2.998	0.083	1.15	0.98-1.36

Supplementary Table 6. Mixed-effects model with IQ and sex effects for the Non-social learning task (N=245) Results of the binomial generalized linear mixed model (GLMM) testing confounding effects of IQ and sex on choice behavior in the Non-social learning task. Predictors of interest are underlined.

	Estimate	*SE*	χ^2	*P*	*Odds Ratio*	*CI*
Age linear	0.183	0.082	4.936	0.026	1.20	1.02-1.41
Age quadratic	0.114	0.080	2.027	0.155	1.12	0.96 -1.31
<u>IQ</u>	0.334	0.075	18.963	<.001	1.40	1.20-1.62
<u>Sex</u>	-0.074	0.078	0.892	0.345	0.93	0.80-1.08

Supplementary Table 7. Parameters of best fitting computational models per game Table with all parameters of the best fitting computational models (i.e., models which include social preferences and decaying learning rates) per game and per age cohort. Results of the non-social game are also included.

		TRUST GAME		
Age cohort	**prior**	**learning rate t=0 (λ_0)**	**decay (τ)**	**decision sensitivity (θ)**
8-11	0.56	0.12	0.00	0.15
12-14	0.54	0.82	1.27	0.12
15-18	0.49	1.00	5.00	0.23
19-23	0.50	0.96	5.00	0.24
		COORDINATION GAME		
Age cohort	**prior**	**learning rate t=0 (λ_0)**	**decay (τ)**	**decision sensitivity (θ)**
8-11	0.71	0.67	1.94	0.63
12-14	0.67	0.61	1.31	0.46
15-18	0.65	1.00	5.00	0.53
19-23	0.68	1.00	5.00	0.69
		NON-SOCIAL LEARNING TASK		
Age cohort	**prior**	**learning rate t=0 (λ_0)**	**decay (τ)**	**decision sensitivity (θ)**
8-11	0.50	0.14	2.99	1.60
12-14	0.50	0.06	1.80	2.93
15-18	0.50	0.05	1.87	4.80
19-23	0.50	0.20	1.43	1.65

Participant instructions

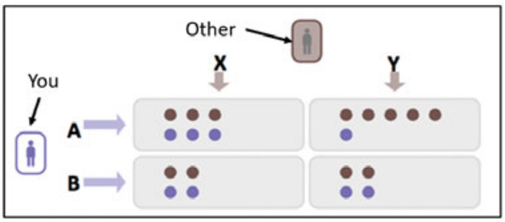
Here we included the instructions for the Trust Game and the non-social learning task. Original instructions were in Dutch. The instructions for the Coordination Game are highly similar to instructions for the Trust Game, and are therefore not included here. Note that on almost every introduction screen for the behavioral tasks, figures of the task were included. Here the figures are only shown when necessary for understanding the accompanying text. The instructions also included some control questions; participants could only continue to the next screen when answered correctly. Full testing and instruction materials can be obtained from the corresponding author.

Instructions Trust Game

The game you will play now has 3 parts. Each part has 30 short rounds.
In each round you will make 1 choice.
On the next screens, the game will be explained.

In each round you play with another student from another school who also participated in this game.
In each round you will both make 1 choice.
In every round, the other is a **new** person.

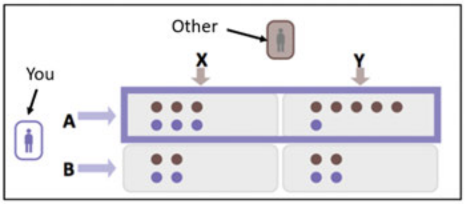
The game will look like this:



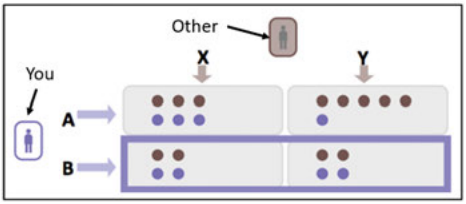
You are the **purple** icon on the left, and you can choose
between the 2 purple arrows (**A** and **B**).
The other is shown on the top of the screen, and can choose between the 2 top arrows (**X** and **Y**).

In each of the four boxes you see dots. Each dot represents 1 point.
The points that you can win with your choice are always **purple**.
The points that the other player can win, have the other color.

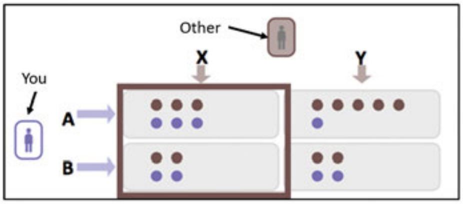
In every round you will make a choice between **A** and **B**.
The other will make a choice between **X** and **Y**.
Your choices **together** determine how many points you and the other win.



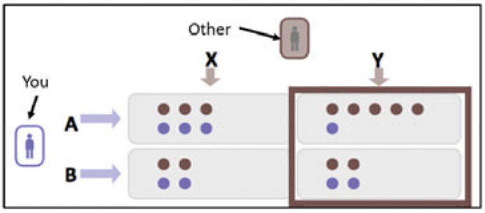
If you choose the **purple** arrow **A**, you select the two top boxes.



If you choose the **purple** arrow **B**, you select the two bottom boxes.



The other can choose arrow **X (top)** to select the two boxes on the left.



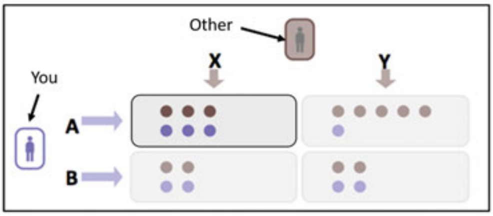
The other can choose arrow **Y (top)** to select the two boxes on the right.

The number of points **<u>you</u>** win, depends on your choice (**A** or **B**), but <u>also</u> on the *other player*'s choice (**X** or **Y**).

The number of points **<u>the other player</u>** wins, depends on the other player's choice (**X** or **Y**), but also on *your choice* (**A** or **B**).

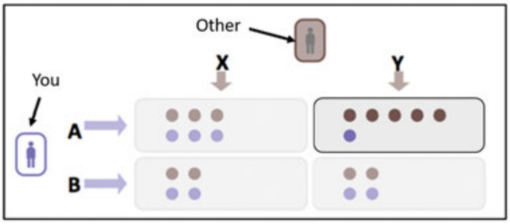
Only *after* you submit your choice, you can see the other's choice.

For example:



Suppose that you choose **A**, and the other chooses **X**:
- You would win **3 points**
- And the other would also win **3 points**

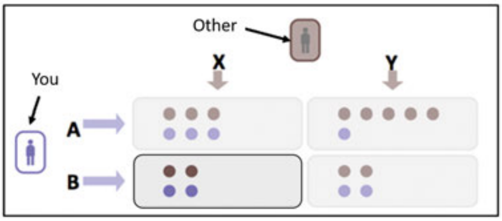
For example:



Suppose that you choose A, and the other chooses Y:
- You would win **1 point**
- And the other would win **5 points**

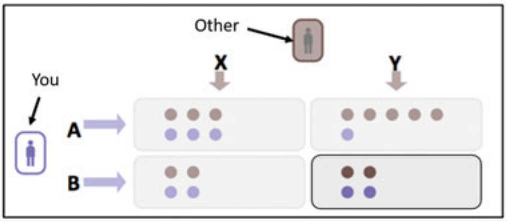
2

For example:



Suppose that you choose B, and the other chooses X:
- You would win **2 points**
- And the other would also win **2 points**

For example:



Suppose that you choose B, and the other chooses Y:
You would win ...... points (fill in)
And the other would win ...... points (fill in)

That is correct!

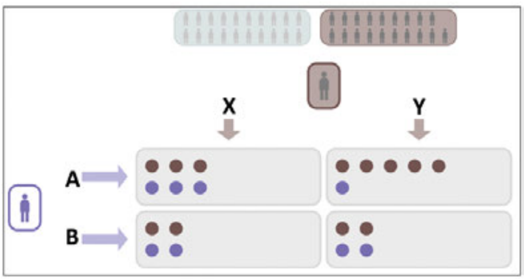
After you see what you and the other have won, the round is over and you will play with a **new person**.

Important: The choices of the other players are made previously by other students from another school.

At the end of the game, the computer will select 5 random rounds.
Each point in those 5 rounds is worth 1 lottery ticket.
After all games, we will draw 1 lottery ticket from all lottery tickets at your school.
The winner receives the gift voucher!
So the more points you have, the larger your chance to win.

The other players can also earn lottery tickets with their choices. With the lottery tickets they also have a chance to win a gift voucher at their school.
Remember: your choices may affect the number of points **you** can win, but they may also affect the number of points the **others** can win.

Environments

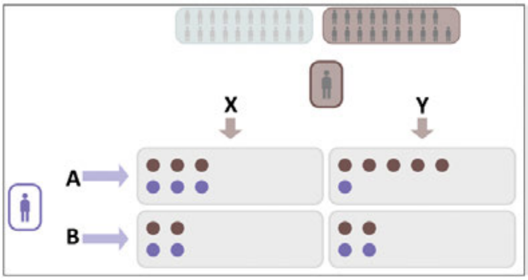


There are 2 environments of other players, each with their own color.
The color of the other player's icon tells you what environment they are in.

In one environment, players usually choose X (left), and in the other environment players usually choose Y (right).

In each round you will play with a new player from 1 of the 2 environments.

Check Question



Suppose that you choose **B** and the other chooses **X**.
How many points would you win? (fill in)____
How many points would the other win? (fill in)____

You have correctly answered the check question!
There will now be 2 practice rounds before you start the real game.

Make your choice by clicking on 1 of your arrows. Then click 'Confirm' at the bottom of the page.

Next, you can see the other's choice, and how many points you and the other have won in this round. Then click 'Continue' to start with the next round.

{2 practice rounds}

Check question
Which environment did the Other player belong to?
If you don't remember, please click back.

The game is about to start.
Do you have any questions? Please ask the researcher now.
You can click **start** if you understand the game.

Try to win as many points as possible by paying close attention to what the other players are doing!

End of part 1

You are finished with part 1 of the game!

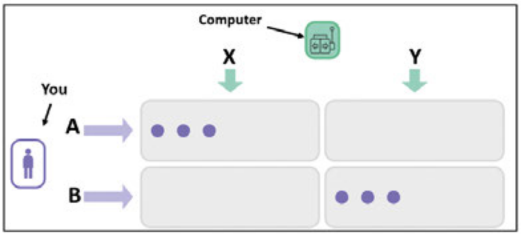
Instructions Non-social learning task

Part 3

In Parts 1 and 2 you were playing with other people.

In Part 3, you will not be playing with other people. Instead, you will play with computers.

The game will look like this:



You are shown in **purple** on the left, and you can choose between the two purple arrows (A and B).

The computer can choose between the **arrows** on the top.

Your points are the **purple** dots.

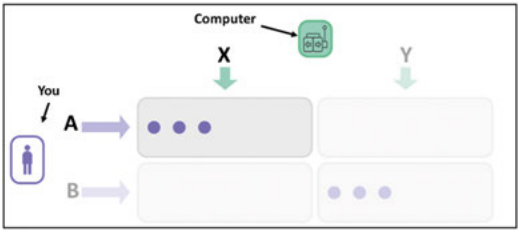
As before, you will choose A or B (top or bottom boxes)

We have programmed the computer to choose X or Y (left or right boxes)

Your choice AND the computer's choice together determine how many points you will win.

Important: the number of points you can win with your choice is different than in the previous games.

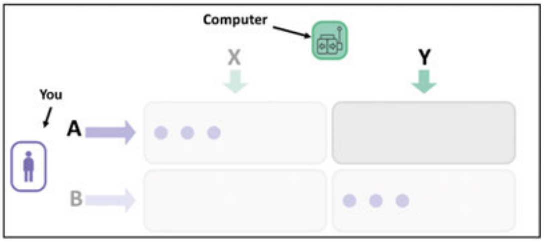
For example,



If you choose A and the computer chooses X:

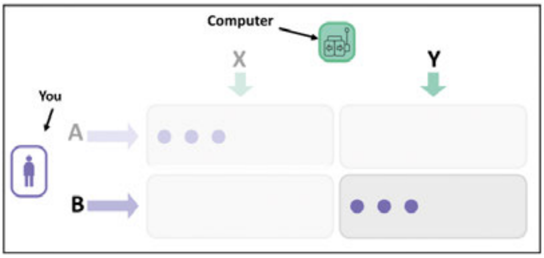
You would win **3 points**

For example,



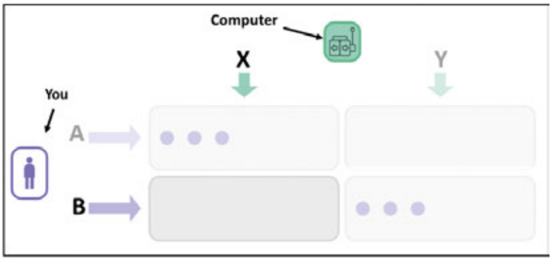
If you choose A and the computer chooses Y:
You would win **0 points**

For example,



If you choose B and the computer chooses Y:
You would win **3 points**

For example,

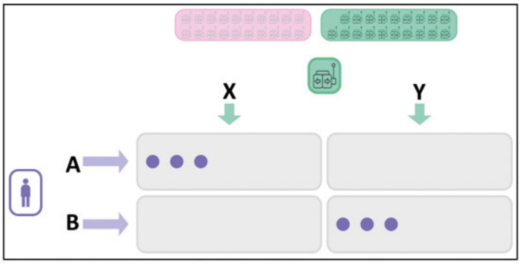


If you choose B and the computer chooses X:
You would win ____ **points** (fill in)

That is correct!
After you see what you have won, the round is over and you will play with a **new computer**.

At the end of the game, 5 rounds will be randomly selected.
Again, each point in the selected rounds is worth 1 lottery ticket.
Remember that you can win the gift voucher.
The more points you have the larger your chance of winning.

Environments



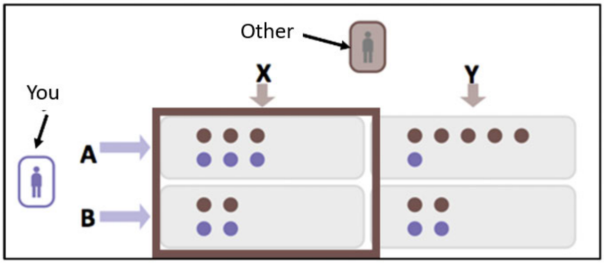
There are 2 environments of computers, each with their own color.
The computer's color tells you what environment the computer is in.
In one environment the computers usually choose **X** (left), and in the other environment the computers usually choose **Y** (right).
In each round you will play with a new computer from 1 of the 2 environments.

Click **Start** to start the game.

Prior expectations

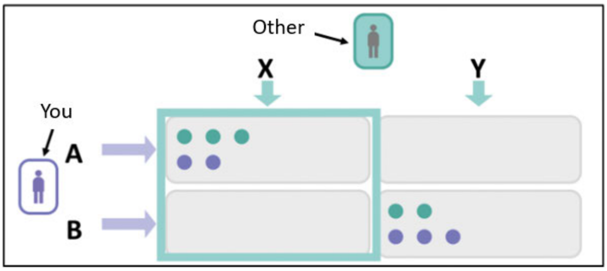
At the end of the learning task instructions, right before the start of the task, we asked about the prior expectations of the participants. This was only done for the social games (Trust Game and Coordination Game).

Prior expectations Trust Game



We are curious about what you think of the other players in this game.
Suppose that there are 10 other players, how many of these 10 do you think will choose X?

Prior expectations Coordination Game



We are curious about what you think of the other players in this game.
Suppose that there are 10 other players, how many of these 10 do you think will choose X?

3

Chapter 3

Can I (still) trust you? Examining adolescents' learning about others' trustworthiness

This chapter is in preparation as:

Westhoff, B., Blankenstein, N. E., Crone, E. A, & van Duijvenvoorde, A. C. K. Can I (still) trust you? Examining adolescents' learning about others' trustworthiness

Abstract

Across adolescence, social interactions with others increase in importance and complexity. For building positive social relations it is important to be able to learn whom (not) to trust and to quickly adjust to changes in other people's trust behavior. One's trust learning abilities may be affected by their experienced parenting practices. Here, we studied the development of social trust learning and social reversal learning in 10-24 year-olds, and the effects of self-reported experienced parenting practices. We used an adapted version of a trust game to assess how adolescents learn about trustworthy and untrustworthy social environments, and flexibly adjust their own trust behavior accordingly. Results showed age-related improvements in overall trust learning performance. However, participants performed better at learning whom not to trust than learning whom to trust. In the reversal block, others' trust levels reversed unannouncedly. Here, participants performed better when switching their behavior to an untrustworthy environment than to a trustworthy environment, which was particularly prominent for the younger ages. Moreover, in this reversal block, trust learning performance in the untrustworthy environment was reduced for participants who reported having experienced poorer parental monitoring. Together, the current study provides insights into the age-related differences trust (reversal) learning across adolescence, and suggest that one's family environment may relate to adolescent' social trust learning abilities.

Introduction

Adolescence is a life phase in which the social environments become more diverse (i.e., school, sports clubs, social gatherings) and social interactions become increasingly important and prevalent (Blakemore & Mills, 2014; Crone & Dahl, 2012; Sawyer et al., 2018). Moreover, social-cognitive skills continue to improve across adolescence (Crone & Dahl, 2012; Dumontheil et al., 2010). An important aspect in building reciprocal social relations is making adequate social decisions. An important social decision is whether to show trust in others. That is, when your decision to trust someone is reciprocated, this may contribute to cooperative social interactions, and ultimately result in a positive social relationship. However, when your trust is violated, you may become less likely to trust the other to prevent wasting your resources. Thus, it is important to be able to learn whom and whom not to trust. Besides learning whom to trust, one should also be able to quickly adjust to changes in other people's behavior. That is, our social world is dynamic, and others may change their trustworthiness, calling for a shift in strategies and subsequent social decision-making. The current study examines how children, adolescents, and young adults (10-24 y.o.) learn about others' trustworthiness, and adjust their trusting behavior when others' trustworthiness levels change.

Trust decisions and trust learning across adolescence

In the past years, multiple studies on trust and trust learning have been conducted. To study how people learn about the trustworthiness of others, these studies have typically used economic games such as the trust game (Berg et al., 1995). Although multiple variations in the specific setup are possible (e.g., one-shot games versus multi-round games), the trust game allows studying trust decisions in a controlled way, across a wide age range. Several studies using a trust game did not observe age-related differences in trust behavior across adolescence (Fett, Shergill, et al., 2014; Lemmers-Jansen et al., 2017; van de Groep et al., 2018). However, this is suggested to be due to their included age range, which did not include (late) childhood (Burke et al., 2020; Li, 2017). Several other cross-sectional studies did show age-related increases in trust behavior across adolescence (Fett, Gromann, et al., 2014; Sutter & Kocher, 2007; van den Bos et al., 2010; van den Bos, van Dijk, et al., 2012). Besides these cross-sectional studies, also a recent longitudinal study that investigated trust learning when confronted with untrustworthy others in early adolescents (12-15 y.o.) observed an age-related improvement (Schreuders, Buuren, et al., 2021). In our recent study, we targeted an adolescent sample with a broad age range (10-24 years), and examined interactions with both trustworthy and untrustworthy others (Westhoff et al., 2020). Here, across adolescence, learning not to trust untrustworthy others slightly improved, whereas learning to trust trustworthy others improved markedly. Together, these findings suggest that from late childhood into adolescence, the sensitivity to detect the level of others' trustworthiness improves, which adolescents can increasingly use to adaptively adjust their behavior in repeated social interactions. The age-related improvement in adjusting to trustworthy (Westhoff et al., 2020), and untrustworthy others (Schreuders, Buuren, et al., 2021; Westhoff et al., 2020) may depend on social-cognitive development such as perspective taking and inequality aversion (Fett, Shergill, et al., 2014; van de Groep et al., 2018; Westhoff et al., 2020), and learning processes (Westhoff et al., 2020). However, the developmental differences in *dynamic* trust learning are not yet well understood.

Reversal trust learning

An essential part of being able to adaptively navigate our social world is the ability to respond to changes in other people's behavior and update our formed beliefs accordingly. That is, if the trustworthiness levels of others change, it may be costly or wasteful if one does not adjust their behavior to the changing social environment. Cognitive flexibility – the ability to respond adaptively towards changing environmental demands (Izquierdo et al., 2017; Peters & Crone, 2014) – in learning is often studied using (non-social) probabilistic reversal learning paradigms. In these paradigms, the reward probabilities change (e.g. from low to high and vice versa), and participants' performance after such reversals are of interest, with higher performance indicating greater cognitive flexibility that benefit reversal learning. Numerous reversal learning studies have been conducted in adult and clinical samples to examine cognitive flexibility (see (Izquierdo et al., 2017; Uddin, 2021) for reviews). A previous developmental study using a non-social probabilistic reversal learning paradigm has shown that adolescents outperformed children and young adults on reversal learning (van der Schaaf et al., 2011). Moreover, another study showed that, compared to adults, adolescents were quicker at adjusting their behavior when the feedback was more negative than expected (Hauser et al., 2015), indicating increased cognitive flexibility in adolescence. Together, these studies point towards adolescence as a phase of heightened cognitive flexibility in learning, especially when outcomes are more negative than expected. Yet, to the best of our knowledge, reversal learning has not yet been studied in a social context across development. Here, we build on our previous study on learning whom (not) to trust (Westhoff et al., 2020) and extend this with a reversal learning manipulation to examine the development of trust learning and trust reversal learning in trustworthy and untrustworthy environments across adolescence.

Parenting practices

Given the vital role of adaptive trust behavior for healthy social interactions and relations (Güroğlu, 2021; Uchino, 2009), it is important to examine the factors that influence the development of trust (learning) across development. The caregiving environment is likely to be a particularly important factor, as previous findings have shown that negative parental practices may shape cognitive development, resulting in reduced cognitive flexibility and learning difficulties (Savitz et al., 2008; Scheuplein et al., 2021). It has been widely recognized that if people are raised in a warm and safe environment, this contributes to positive long-term outcomes, such as individual wellbeing, social connections, and educational achievements (Ioannidis et al., 2020; Smetana & Rote, 2019). However, households with mostly negative parenting practices (e.g., expressing negative emotions, handling roughly), physical and emotional neglect, or even maltreatment (e.g., physical and emotional abuse), may result in more internalizing and/or externalizing behavioral problems early in life (Cecil et al., 2012; Jaffee, 2017; Smetana & Rote, 2019). In addition, individuals risk long-term consequences, such as a hyperactive stress response, low self-esteem, impaired mental health, and impaired social functioning (Gobin & Freyd, 2014; McCrory & Viding, 2015; Overbeek et al., 2020). However, it is yet unknown whether environmental variables such as parenting practices also affect adolescent's social trust learning. One hypothesis is that growing up in a volatile environment with negative and/or inconsistent parenting practices may make people more sensitive to social cues, leading individuals to be hypersensitive to the outcomes (both positive and negative) of social interactions. This pattern would lead individuals to update their beliefs about others too quickly (*cf*. tit-for-tat strategy), hampering social learning in general (e.g., van Harmelen et al., 2014). Alternatively, growing up with mostly negative parental practices may result in a stronger negativity bias (Toth et al., 2011). Consequently, in these individuals, learning to trust trustworthy others would be hampered compared to learning not to trust untrustworthy others (Hanson et al., 2017). Here, we aim to disentangle these hypotheses by examining the relations between parenting practices, trust learning, and trust reversal learning in a sample of typically developing adolescents (10-18 y.o.). Besides negative parenting practices we also exploratively assessed effects of positive parenting practices on trust (reversal) learning.

The current study

In the current study, we recruited a sample of 160 children, adolescents, and adults (10-24-years old). Participants played a version of the trust game similar to the version we previously used in (Westhoff et al., 2020), which was extended with a reversal learning block, and filled in self-reports on parenting practices (e.g., parental involvement and inconsistent discipline). The trust game consisted of multiple repeated one-shot games, in which participants encountered players from different social environments. These environments showed either low or high levels of trust, and over trials, participants could learn whether to trust a player from a particular environment or not. This set-up enabled us to assess how participants learn about others' trustworthiness level and accordingly adjust their trust behavior to other players in that environment. Note that, although trust choices generally are not a matter of 'good' and 'bad' decisions, in the current setup trust choices can be labeled as more optimal and suboptimal with regard to one's own outcome. Therefore we use the term performance as an indication of how well someone has adjusted to a certain environment.

An ongoing debate is whether social (reversal) learning patterns are specific to learning in a social environment (e.g., Lockwood et al., 2020; Ruff & Fehr, 2014). To allow a direct comparison between social and non-social learning, we additionally included a non-social condition in which participants interacted with slot machines.

The current study aimed to investigate: 1) the age-related differences in learning whom (not) to trust in social and non-social environments, 2) the ability to flexibly adjust behavior towards changing levels of others' trustworthiness (i.e., reversal learning) and its corresponding age-related differences, and 3) the effects of positive and negative parenting practices on trust learning and trust reversal learning.

First, in line with previous studies, we hypothesized an age-related improvement in trust learning across adolescence (Schreuders, Buuren, et al., 2021; van den Bos, van Dijk, et al., 2012; Westhoff et al., 2020), in which learning whom to trust shows greater age-related improvement than for learning whom to distrust (Westhoff et al., 2020). Exploratively, we examined whether these developmental patterns were specific to social trust learning.

Second, considering the development of cognitive flexibility in non-social paradigms across adolescence (Hauser et al., 2015; van der Schaaf et al., 2011), we expected an age-related improvement in the flexibility in learning about others' trustworthiness (reversal learning). As previous studies have observed a negativity bias resulting in faster adjusting to negative than positive outcomes, we expected that participants adjust more easily when a trustworthy environment becomes untrustworthy than vice versa.

Finally, we expected that trust learning and reversal learning performance would be affected for individuals who reported having experienced more negative parenting practices. Specifically, higher ratings of self-reported negative parenting practices would potentially result in impaired trust learning performance in both the trustworthy and untrustworthy environment (volatility hypothesis). Alternatively, individuals who reported having experienced more negative parenting practices would show an asymmetry in learning, in which learning whom to trust (or who switches from untrustworthy to trustworthy) is more impaired compared to learning to distrust untrustworthy others (negativity bias hypothesis).

Methods and Materials

Participants

In total, 160 participants between ages 10 and 24 took part in this study. Participants were recruited through local advertisements and schools. The majority of the participants (96.2%) were born in the Netherlands. Social-economic status (SES), based on the highest achieved parental educational level, indicated that most participants were raised in families with a high (58.0 %) or middle (36.9 %) SES (low SES = 5.1%). Three participants were excluded from analyses because they only filled in the questionnaires but did not perform the learning task.

The final sample, therefore, consisted of 157 healthy participants (78 boys, 79 girls) aged 10-24 years (Mean = 17.51, SD = 4.33; see Figure S1A). The distribution of boys and girls was balanced across age cohorts ($\chi^2(4) = 0.21$, $p = .995$). The IQ scores, estimated with the Similarities and Block Design subtests of the WISC-V (Wechsler, 2008) and WAIS-IV (Wechsler, 2014), were within the normal range varying between 80 and 135 (mean IQ = 106.85, SD = 10.95), and did not correlate with age ($r = -0.12$, $p = .142$). Control analyses showed that sex and IQ did not confound performance on trust learning or reversal learning, and did not influence any of our observed age-related differences (see Supplementary Tables 1 and 3). For the analyses focusing on the effects of parenting practices on trust learning and reversal learning, we only included participants up to 18 years old, as the parenting questionnaire has only been validated for these ages (Frick et al., 1999). This sample consisted of 94 participants aged 10.0 – 18.8 (Mean = 14.49, SD = 2.56) for trust learning and 93 participants for reversal learning analyses.

All procedures were approved by the Medical Ethics Committee of the Leiden University Medical Centre (reference: NL56438.058.16) and performed in accordance with the relevant guidelines and regulations. Adult participants and caregivers of minors provided written informed consent, and minors provided written assent. This study was part of a larger imaging study (data not included in the current article). Participants were therefore screened for MRI contraindications and psychiatric or neurological disorders, and had normal or corrected-to-normal vision.

Procedure

First, participants filled out questionnaires at their homes before the experimental session, via Qualtrics (www.qualtrics.com). During the experimental session, participants were first accustomed to the MRI environment using a mock scanner. Subsequently, they received instructions on the learning task in a quiet laboratory room. Instructions for the task were displayed on a screen and were read out loud by an experimenter. Within the instructions, control questions were incorporated regarding the outcomes of the task to ensure understanding of the point distributions (i.e., indicating how many points each player was winning in a certain choice combination). If participants failed one of the control questions, the instruction was repeated until participants understood the procedure of the game. Participants played 8 practice trials in both the social and non-social conditions (16 trials in total) to familiarize themselves with the game and its timings. In these practice trials, the behavior of both environments was 50% trustworthy to avoid learning effects that could potentially affect behavior in the actual learning task. The outcomes of the practice trials were not paid out. The actual learning task was performed in the MRI scanner; despite handedness, they responded with their right index and middle finger using a button box.

During the experimental session, besides subtests of the WISC-V (for participants ≤ 16 y.o.) and WAIS-IV (for > 16 y.o.), also other measures (not relevant to the current study) were obtained. After completion of the experimental session (3-3.5 hour), participants received a goodie bag and financial compensation. This compensation consisted of a flat rate, which amount was age-dependent (€20 for 10-12 y.o.; €25 for 13-17 y.o.; €30 for 18-24 y.o.) and a bonus (ranging €5 - €15) based on performance in all tasks (part of a larger study) during the experimental session.

Trust Learning task

Participants completed an incentivized economic game: A trust game, with a within-subject social condition and a non-social condition (Figure 1). The game was composed of 28 trials in total: each trial was a one-shot game with a new anonymous player (indicated with a new avatar). In every trial the participants chose between 2 options (A or B) to distribute points between themselves and the other. In the social condition, the other player was an unknown peer, whereas in the non-social condition, the other player was a slot machine. After their decision, participants could see the choice of the other player (X or Y) and the outcomes for themselves and the other player. Outcomes for self and the other resulted from their combined choices. The social condition of the trust game (Figure 1B) was characterized by payoff matrix $\begin{bmatrix} \mathbf{3}, 3 & \mathbf{2}, 2 \\ \mathbf{1}, 5 & \mathbf{2}, 2 \end{bmatrix}$, with earnings for self indicated in bold. The non-social condition of the trust game (Figure 1D) was characterized by a similar payoff matrix, but only the participants received payoffs.

In each of the conditions, two environments were consisting of 14 players each. Environments were set up as such that we created a 'Trustworthy' (78.5% trustworthy choices, i.e., 11 out of 14 trials) and an 'Untrustworthy' environment (78.5% untrustworthy choices, i.e., 11 out of 14 trials) (see Figure 1). The color of the players indicated to which environment they belonged. It was randomized across participants which color was related to the trustworthy or untrustworthy environment. Over the course of the trials, participants could learn the tendency of choosing X for each environment of other players and adjust their responses accordingly. Participants were incentivized as their points were converted to a financial bonus ranging €2 - €8.

Participants could maximize their earnings by choosing A ('trust'; top row) when matched with a member of the Trustworthy environment, and choosing B ('distrust'; bottom row) when matched with a member of the Untrustworthy environment. The inconsistent choices within an environment (e.g., Y when playing with someone of the environment that generally prefers X) were semi-randomized and appeared between trials 2 and 4, between trials 6 and 8, and between trials 10 and 12. Interactions with players from trustworthy and untrustworthy environments were presented in semi-random order, with the limitation that an environment can appear twice in a row at most.

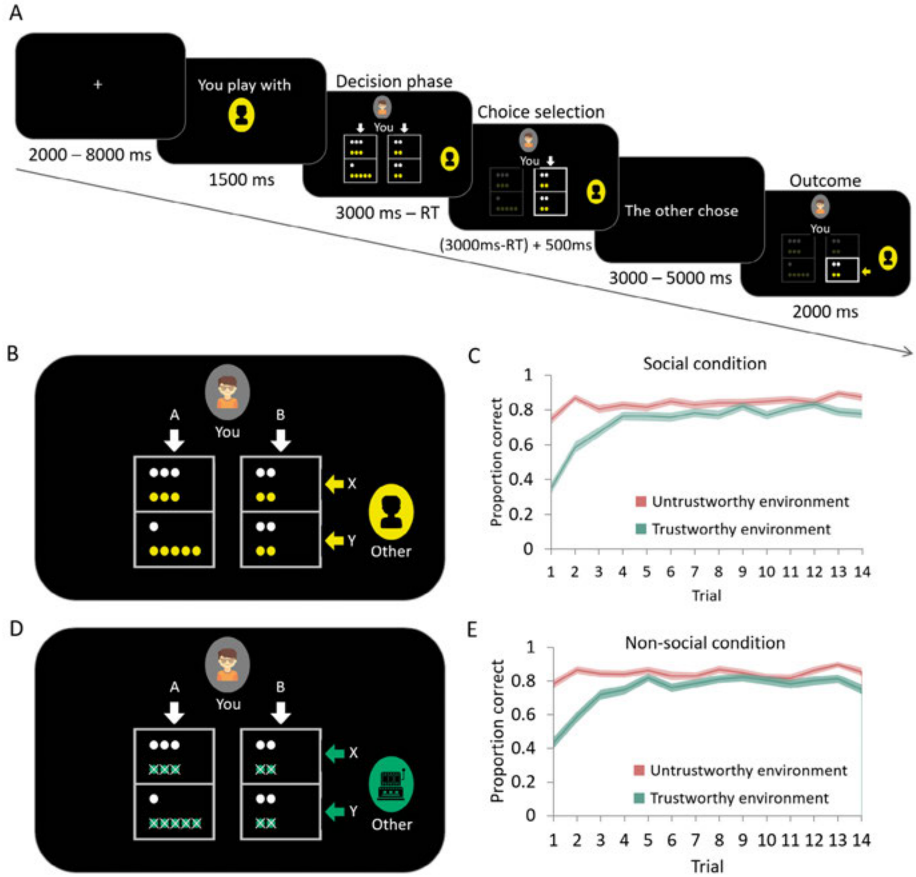


Figure 1. Task assessing learning about trustworthy and untrustworthy environments. **(A)** Example trial. The participant (shown on top) can choose between the left and right columns (arrow A or B). After choice selection, the participant is shown the choice (top or bottom row, indicated with arrow X or Y) of the other player (shown on the right). The combined choices of the participant and the other player determine the monetary outcome for both players (number of dots; white dots for the participant, colored dots for the interaction partner). The background color of the other player indicates to which of the two environments they belong. In each trial there was a one-shot game with a new anonymous player, indicated with a new avatar. Note that in the non-social condition, the interaction partner (slot machine) does not receive any outcome, as indicated with the crosses through the colored dots (see panel d). **(B)** In the social condition, participants interact with players from a 'Trustworthy' environment (who tend to choose X) or an 'Untrustworthy' environment (who tend to choose Y). Participants' own monetary payoffs are maximized by choosing to trust (choose A) a player from a Trustworthy environment, and to withhold trust (choose B) from a player from the Untrustworthy environment. **(C)** Proportion correct choices over trials per social environment averaged over the first and second social block, and pooled across all participants. Over trials, participants adjusted their choices by directing their trust towards players from the Trustworthy environment, and away from players from the Untrustworthy environment. **(D)** In the Non-Social condition, participants' monetary payoffs are also maximized by matching the choices of their co-players. Again, the environments differ in their tendencies to choose either X or Y. Similarly to the social condition, participants' own monetary payoffs are maximized

by choosing to trust (choose A) a player from a Trustworthy environment (prefers X), and to withhold trust (choose B) from a player from the Untrustworthy environment (prefers Y). **(E)** Proportion correct choices over trials per environment averaged over the first and second block, and pooled across all participants. Overall, participants learned to adjust their choice behavior to the non-social environments. Shaded areas in panels c and e represent standard errors of the mean (s.e.m.).

For the analyses, participants' decisions were coded as either correct or incorrect. That is, choosing to trust (A) when confronted with an interaction partner from a *trustworthy* environment (tends to choose X), or choosing to withhold trust (B) when interacting with a player from an *untrustworthy* environment (tends to choose Y), is coded as a correct decision (coded as 1). Whereas choosing to trust (A) when confronted with an interaction partner from an *untrustworthy* environment, or choosing to withhold trust (B) when interacting with a player from *trustworthy* environment, is coded as an "incorrect" decision (coded as 0). Note that due to the probabilistic nature of the task, a round coded as incorrect can result in an outcome that resembles a correct decision (e.g., outcome A-X when playing with an untrustworthy environment), and vice versa.

In total, participants completed four blocks of 28 trials (14 trials per environment), with a short break in between. In each block, participants were confronted with two new environments, indicated with new colors. Participants completed two social and two non-social blocks. The order of these blocks was alternated and counterbalanced between participants (i.e., either: social – non-social – social – non-social, or: social – non-social – non-social – social). These differences in block order did not affect performance (*ps* > .09).

The fifth block (28 trials, 14 per environment), included a between-subject manipulation to assess reversal learning (see Figure S2). That is, participants encountered new players from the same environments as the previous block (block four). However, unbeknownst to the participants, the new players switched their response tendency. That is, the Trustworthy environment from block 4, became an Untrustworthy environment in block 5, and vice versa. Given the counterbalanced order of the blocks, half of the subjects encountered a social reversal, and the other half a non-social reversal.

Parenting questionnaire

As a measure of parenting practices, participants filled out the Alabama Parenting Questionnaire (APQ) (Frick et al., 1999). This questionnaire consists of 42 items across five domains: Parental Involvement (10 items per parent; e.g. for maternal involvement: "You play games or do other fun things with your mum", Cronbach's alpha: .744; e.g., paternal involvement, Cronbach's alpha: .852), Positive Parenting (6 items; e.g., "Your parents tell you that you are doing a good job"; Cronbach's alpha: .788), Poor Monitoring/Supervision (10 items; e.g., "You go out without a set time to be home"; Cronbach's alpha: .665), Inconsistent Discipline (6 items; e.g., "Your parents threaten to punish you and then do not do it"; Cronbach's alpha:

.511). The Corporal Punishment subscale was not administered in the current study. All items can be answered on a 5-point scale (i.e., (1) never, (2) almost never, (2) sometimes, (4) often, (5) always). The Positive Parenting, Maternal Involvement, and Paternal Involvement scales reflect more positive aspects of parenting, while the Inconsistent Discipline and Poor Monitoring/Supervising scales reflect more negative aspects of parenting. The target audience for the APQ is 6 – 18 year-olds, therefore in analyses concerning the APQ, we only included participants up to 18 years. Note that, although we have included a typical developing sample, the variation in these measures (see Figure S3) was deemed sufficient to probe individual differences in parental relations.

Statistical analyses

To analyze trust learning and reversal learning in the social and non-social condition of the trust game, we fitted logistic generalized linear mixed models (GLMMs) to the 'correct' decisions made. First, we assessed learning in social and non-social conditions (block 1-4; N = 157). This GLMM included fixed effects of environment (i.e., Trustworthy environment, Untrustworthy environment), age in years (both linear and quadratic polynomial), and condition (i.e., social, non-social), as well as the two- and three-way interactions between these predictors.

Second, we assessed social and non-social reversal learning (block 5; N = 155). This GLMM included fixed effects of environment (i.e., Trustworthy environment, Untrustworthy environment), age in years (linear and quadratic polynomial), and condition (i.e., social, non-social).

Third, we assessed relations with parenting practices on trust learning for the participants up to 18 years old. A GLMM on blocks 1-4 (N=94) included main effects of environment (i.e., Trustworthy environment, Untrustworthy environment), condition (i.e., social, non-social), all parenting subscales (Positive parenting, Poor monitoring, Inconsistent discipline, Maternal involvement, Paternal involvement), as fixed effects, as well as the two- and three-way interactions between these predictors. As this analysis focused on individual differences in parenting, age (linear) was included as covariate. A similar GLMM was performed on reversal learning (block 5, N = 93). Note that, although some of these parenting subscales are correlated (see Table S5), there is no multicollinearity (i.e., VIF values < 1.9).

All GLMM models included a random-intercept per participant to handle the repeated nature of the data. Where appropriate, the environment (trustworthy, untrustworthy) and condition (social, non-social) was entered as a random slope in our analyses to handle the differences between individuals in their responsiveness to learning different levels of trustworthiness.

Mixed-effects analyses were conducted in R 4.0.5, using the lme4 package (Bates et al., 2014; R Core Team, 2020). All numeric variables were mean-centered and scaled, and categorical predictor variables were specified by a sum-to-zero contrast (e.g., sex: − 1 = boy, 1 = girl). For all models the optimizer "bobyqa" (Powell, 2009) was used, with a maximum number of

1×10^5 iterations. P-values are obtained with the lmerTest package (Kuznetsova et al., 2017). Full statistics are reported in Tables S1-S5.

Results

Age-related improvement in learning whom (not) to trust in social and non-social environments

Our first aim was to assess age-related differences in adjusting to trustworthy and untrustworthy environments in the social and non-social condition of the trust game. One-sample t-tests showed that participants performed above change level (50%) in each block, in both the trustworthy and untrustworthy environments, and in both conditions (*ts* > 12.8, *ps* < .001), demonstrating that they are able to learn to trust trustworthy others, and to withhold trust from untrustworthy others over trials. Using a mixed-effects model, we observed that older participants performed better than younger participants (main effect of Age linear, $B = 0.312$, $p < .001$, Figure 2, Table S1).

Figure 2. Age-related improvement in trust learning performance. Proportion correct across age when playing with a trustworthy and an untrustworthy environment, **(A)** in a social condition, and **(B)** in a non-social condition. The age-related improvements are similar for both environments and both conditions. Note that age was scaled in the analyses, therefore the age values on the x-axes are an indication of the values from the mixed-effects models. Shaded areas indicate the 95% confidence interval.

Although overall performance was somewhat better in the non-social condition than in the social condition (main effect of Condition, $B = 0.057$, $p = .038$), this did not differ with age (Age linear x Condition, $p = .350$). Moreover, participants performed better when learning to withhold trust from untrustworthy others than when learning to trust trustworthy others (main effect of Environment, B = 0.408, p < .001). This pattern was similar for the social and non-social condition (Condition x Environment, B = -0.008, p = .724), and did not change with age (Age x Environment, B = -0.009, p = .870; Age x Condition x Environment, B = 0.038, p = .076). Together, these results suggest that participants find it easier to learn to adjust to an untrustworthy environment than a trustworthy environment.

Reversal learning: flexibility in learning about others' trustworthiness

Our next goal was to assess age-related differences in trust reversal learning in the social and non-social condition (see Table S2). A mixed-effect model revealed that participants performed better when switching to an untrustworthy environment (Trustworthy → Untrustworthy reversal) than when switching to a trustworthy environment (Untrustworthy → Trustworthy reversal) (main effect of Environment, B = 0.403, p < .001), suggesting that participants were more sensitive for signaling a change towards untrustworthy than to trustworthy behavior. Moreover, results showed an Age linear x Environment interaction (B = -0.139, p = .049, see Figure 3A).

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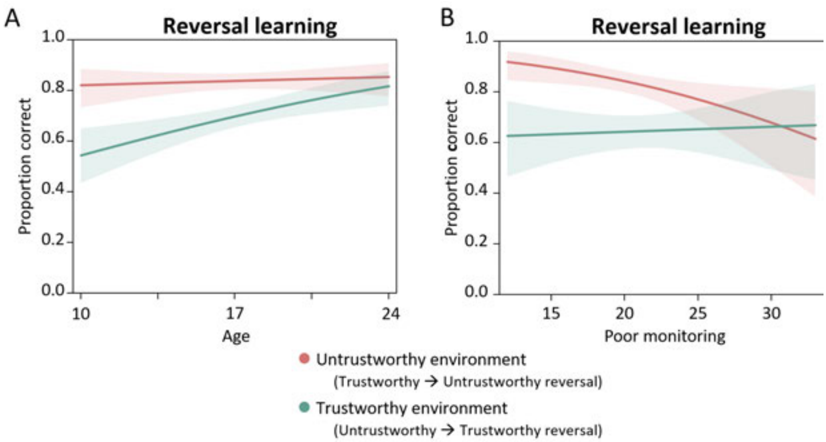


Figure 3. Reversal learning: Developmental asymmetry and differential effect of poor monitoring **(A)** Proportion correct across age for interacting with players from a Trustworthy and an Untrustworthy environment in the reversal block (10-24 y.o., N = 155). Performance across age is stable when interacting with the untrustworthy environment (which was trustworthy prior to the reversal), whereas performance shows age-related improvements when playing with the trustworthy environment (which was untrustworthy prior to the reversal). Note that age was scaled in the analyses, therefore the age values on the x-axis are an indication of the values from the mixed-effects models. **(B)** Relation between proportion correct and poor parental monitoring in the reversal block (10-18 y.o., N = 94). Higher levels of reported parental poor monitoring result in lower differentiation in performance for learning to trust trustworthy others and to withhold trust from untrustworthy others. In both panels, effects are collapsed across conditions and shaded areas indicate the 95% confidence interval.

Post-hoc tests per environment revealed that participants from all ages adjusted well to an untrustworthy environment (Trustworthy → Untrustworthy reversal; main effect of Age, $B = 0.045$, $p = .708$), whereas adjusting to a trustworthy environment (Untrustworthy → Trustworthy reversal) was subject to age-related improvements (main effect of Age, $B = 0.331$ $p = .001$). When controlling for performance in the pre-reversal block, this pattern remains (see Table S2). Finally, we observed that reversal learning did not differ between the social and non-social condition (main effect of Condition, $p = .669$; Age linear x Condition, $p = .268$; Environment x Condition, $p = .551$). Together, these findings show that it is harder to adjust trust behavior towards interactions with a trustworthy environment, versus behavior towards interaction with an untrustworthy environment, and that this pattern was particularly pronounced for the younger participants.

Individual differences in parenting affect trust learning and reversal learning

Our final aim was to assess whether parenting practices affected performance in trust learning and reversal learning in participants up to 18 years old (see Table S3). In a mixed-effects model assessing trust learning in block 1-4, we did not observe main effects of the parenting subscales, nor interactions with environment or condition (p's $> .06$, see Table S3).

Finally, we assessed the effects of parenting on reversal learning. Results showed a Reversal type x Poor monitoring interaction ($B = -.029$, $p = .023$), which indicates that participants who reported having experienced poorer parental monitoring showed little differentiation between the Untrustworthy and Trustworthy environment in the reversal block, whereas participants who reported *lower* levels of poor monitoring show a larger differentiation (see Figure 3B). The other parenting subscales did not affect learning performance in the reversal block (see Table S4).

Discussion

The aim of this study was to investigate (1) the development of learning whom (not) to trust across adolescence in social and non-social environments, (2) the ability to flexibly adjust trusting behavior when others' trustworthiness levels change (reversal learning), and its corresponding age-related differences, and (3) how reported parenting practices affect trust learning and reversal learning performance. To this end, we used an experimental paradigm based on the traditional trust game, which enabled us to assess how participants learn about others' trustworthiness and adjust their own trust behavior accordingly. The results of this study revealed that participants' performance in both environments were above change level, indicating that they were able to learn to trust trustworthy others, and to withhold trust from untrustworthy others over trials. Moreover, as expected, performance in trust learning improved with age.

Also, people adjusted better to environments that required not trusting others, compared to environments that required trusting others. Contrary to our expectations, learning performance in untrustworthy versus trustworthy environments did not differ across age. Second, as expected, we observed that in the reversal learning block, learning to trust others (who were untrustworthy before reversal) was more difficult than learning whom not to trust (who were trustworthy before reversal). In addition, we observed that this effect was more pronounced for younger participants. Third, parental poor monitoring was found to affect reversal learning, as higher ratings of poor parental monitoring/supervision were related to reduced performance in switching towards an untrustworthy environment. Finally, although overall performance was slightly better in the non-social than the social condition, we did not observe any differences between the social and non-social condition in reversal learning performance, nor in effects of age or parenting practices. The discussion is organized alongside these main findings.

Learning whom (not) to trust across adolescence

Across our learning and reversal learning paradigm, we observed an asymmetry in performance depending on the environment people needed to adjust to. Specifically, participants performed better at learning whom *not* to trust than learning whom to trust. Similarly, in our reversal learning block participants were better at adjusting their trust behavior to untrustworthy others that were previously trustworthy, than vice versa. These results suggest that participants were more sensitive for signaling and adjusting to untrustworthy behavior than to trustworthy behavior. With regard to trust learning, such an asymmetry was also observed in our previous study which showed better performance for learning whom not to trust than for learning whom to trust in 8-23 year-olds (Westhoff et al., 2020). Also in adults, this bias has been observed (e.g., Siegel et al., 2018; Vanneste et al., 2007). For example, a recent comprehensive study on the traits of 'bad' and 'good' others in adults showed that participants were more quickly and accurately in detecting the bad others than the friendly others, and their impressions of the former were more rapidly updated as well (Siegel et al., 2018). Such a *negativity bias* is a general principle that has been found across a broad range of psychological phenomena, and it is thought that it would generally be adaptive for individuals to respond more strongly to negative than to positive actions or outcomes (Baumeister et al., 2001). Our results suggest that this negativity bias extends to trust learning.

We observed little age-related differences in learning to adjust to trustworthy or untrustworthy environments. Based on previous findings we expected the asymmetry in learning to adjust to trustworthy versus untrustworthy environments to be larger for younger ages (Westhoff et al., 2020). In reversal learning, however, we did observe this asymmetry: performance in adjusting towards an untrustworthy environment (trustworthy before reversal) was stable across ages, whereas adjusting to the trustworthy environment (untrustworthy before reversal) showed age-related improvements. Potentially, younger individuals are particularly at a disadvantage in adjusting to an untrustworthy environment if the learning situation is more challenging. That is, the reversal block likely requires more cognitive control, as previously build up stimulus-response associations need to be reversed. This ability to inhibit prepotent responses may depend prominently on brain areas such as the prefrontal cortex which slowly develop across adolescence (Luna et al., 2013). In future research this neural hypothesis should be further supported.

Finally, although adolescent' flexibility has been studied in terms of age-related differences in cognitive flexibility (Crone et al., 2008; Luna et al., 2013; van Duijvenvoorde et al., 2008) and handling volatile environments in reversal learning paradigms (Hauser et al., 2015; Jepma et al., 2020; van der Schaaf et al., 2011), the application in a social environment is relatively unexplored. A recent study examined age-related differences in response to continuously changing (non-social) environments and showed that, compared to adults, adolescents overestimated the environmental volatility (i.e., unpredictable change in stimulus-outcome or action-outcome associations) (Jepma et al., 2020). This overestimation of the volatility of an environment in adolescence may especially be adaptive in this developmental phase as it is characterized by changes in social relations, such as building new friendships, and engaging in a diversity of social environments including school, sports clubs, and social gatherings (Fuligni, 2019). These findings may suggest that adolescents may have a specific advantage to adjusting to highly volatile or unpredictable environments. Whereas the current study informs us on the ability to flexibly change a learned association in a relatively stable learning environment, future studies could study flexibility in social learning more thoroughly by including volatile or unpredictable social environments.

Parenting effects on social reversal learning

An additional aim of the current study was to assess the effects of participants' reported parenting practices on trust learning and social reversal learning. We observed that participants who reported having experienced poorer parental monitoring showed increased levels of trust to untrustworthy others, but only when these others were previously trustworthy. Performance in the trustworthy environments was stable across the range of reported poor monitoring values. These findings contradict the two hypotheses we initially posed: the volatility hypothesis (i.e., hypersensitivity towards both positive and negative social interactions and thus reduced performance in both environments), and the negativity hypothesis (i.e., reduced sensitivity to positive compared to negative social interactions, thus reduced performance in the trustworthy environment only). It is conceivable that other individual differences may have biased the results. For example, poor parental monitoring has been also been related to more disadvantageous risk taking (Pollak et al., 2020), cyberbullying (Pascual-Sanchez et al., 2021) and several other behavioral problems (Racz & McMahon, 2011).

We did not observe any associations between the trust (reversal) learning performance and the other parenting practices (i.e., inconsistent discipline, maternal and paternal involvement, positive parenting); future studies are needed to replicate this null result. One potential factor that may have biased our associations with parental practices is social support. That is, previous research has suggested that social support (high quality, supportive social relations), may buffer the effects of parental maltreatment on several behavioral outcomes (Scheuplein et al., 2021). This may also be true for less severe negative parenting situations. Consequently, participants who reported having experienced more negative parenting practices, may have had a good social support network, and therefore their social learning abilities were less affected. Future studies could investigate this hypothesis by including a focus on the social support network, such as the role of friendship quality. Recent studies combined such social network analyses (social network within the classroom) with choices in a trust game choices. Although social network positions did not affect adaptations of trust behaviors towards untrustworthy others in early adolescents (+/- 12 y.o.) (Sijtsma, Buuren, et al., 2020), in older adolescents (16-18 y.o.) participants with less central social positions were *more* adaptive towards trustworthy others when they expected those others to be untrustworthy (Sijtsma, Lee, et al., 2020). Although one's social network position may not be an indication of the quality of friendships that person has, these findings highlight that social dynamics other than parenting practices may influence trust decisions and trust learning. Moreover, these effects may change across adolescence alongside the stabilization of friendships. The exact mechanisms of how social buffering and risk factors relate to social (reversal) learning need to be confirmed in future (longitudinal) studies.

Social versus non-social learning

In the current study, we assessed whether there are differences between social and non-social trust learning. An active debate in the literature is whether social learning is only dependent on processes that are socially specific, or that it arises solely from general associative (non-social) learning (Heyes, 2012; Lockwood et al., 2020; Olsson et al., 2020; Ruff & Fehr, 2014). Therefore, when studying social learning, an appropriate control condition is essential for falsification purposes. Previous studies have used computer opponents in their control condition (Apps et al., 2013; Ramnani & Miall, 2004; Sanfey et al., 2003). However, as humans may anthropomorphize computers (Nass & Moon, 2000), we attempted to overcome this by using slot machines as an alternative. Thus, as a control condition, we included a similar trust game but with slot machines (not receiving any payoff) as interaction partners to remove the social component of trust learning. Our results showed a main effect of condition, indicating that overall performance in non-social trust learning was better than in social trust learning. However, we did not find a condition difference in reversal learning performance, nor did we find interactions with environment, age, or parenting practices. Our results, therefore, suggest that these social and non-social learning processes are either at least largely overlapping, or, alternatively, distinct subprocesses may have resulted in similar behavioral outcomes (Morton, 2010). There are multiple levels on which social learning may differ from non-social learning on e.g., observed behavior, computational processes such as reinforcement learning, and underlying neural circuitry (Lockwood et al., 2020). Although the current study provided valuable insights on the behavioral level, follow-up studies are necessary to disentangle on which levels and which processes would be uniquely social in the case of trust learning. These studies would benefit from computational modeling and neuroimaging analyses to provide more insights into the mechanistic understanding of the subprocesses involved in trust learning and social reversal learning, and thus are needed to reveal whether there are neurocognitive processes are uniquely involved in *social* (trust) learning.

Limitations and future directions

There are a few limitations that have to be taken into account when interpreting the results. First, although the current sample is relatively large and is evenly distributed across age and sex, it is, however, rather homogenous, especially with regard to ethnicity and SES. Moreover, only typically developing children, adolescents and young adults were included, and the majority of these participants would not have experienced parenting adversity. It is not unlikely that negative parenting practices are related to lower participation rates in scientific studies; research setups that are less demanding for the parents, for example by testing in schools, would improve sampling of these more vulnerable children. Future studies are encouraged to invest in more diverse recruitment, as greater demographic and clinical diversity result in more power to detect effects of individual differences in e.g., parenting experiences on social decision making and (reversal) learning.

Second, the current trust learning paradigm only included interaction partners with low and high levels of trust. However, especially when investigating a sample of participants who have grown up in an unpredictable environment, it would be interesting to include interaction partners who are unpredictable in their trust behavior (i.e., 50% trustworthy) or more volatile in their trust behavior (i.e., often switching from trustworthy to untrustworthy behavior) to resemble more realistic characteristics with regard to their environment's trust behavior.

Moreover, in the current study we only examined interactions with unfamiliar peers. However, interacting with different targets, such as friends, foes, and family members could reveal whether trust learning behavior is differs between different targets. Previous social-decision making studies involving such targets have shown differential effects (Brandner et al., 2020; Schreuders et al., 2018; Spaans et al., 2018, 2019; van de Groep et al., 2020). For example, a recent study showed that adolescents were more prosocial towards their friends and more selfish towards disliked peers (Schreuders et al., 2018). An interesting follow-up study would include different targets in order to shed light on ingroup-outgroup (e.g., friends or parents as ingroup versus strangers as outgroup) processes, and how these affect social learning.

Finally, although we examined age-related and individual differences in social Learning, tracking these factors longitudinally would be powerful and essential for examining true developmental trajectories of social learning (Crone & Elzinga, 2015). Moreover, a longitudinal setup allows for investigating the stability in for example friendships and parental relations, and how they relate to social learning (Schreuders, Braams, et al., 2021). Therefore, future studies would benefit from following these participants with similar learning paradigms (Telzer et al., 2018).

Conclusion

Here, we studied the development of social trust and reversal learning in 10-24 year-olds and included a first step to determine whether individual differences in family environment also affect social (reversal) learning. We observed that adjusting to a trustworthy environment (particularly if those others were untrustworthy before) is more difficult than adjusting to an untrustworthy environment. Particularly for younger adolescents updating their expectations of others' trustworthiness is more difficult than for older adolescents and adults. These findings highlight an increasing cognitive flexibility in learning across adolescence that also extends to a social environment. Finally, parental poor monitoring impacted trust reversal learning. Thus, the environment in which we grow up may affect our future social interactions and how we learn about others. However, adolescence is a developmental phase in which peers play a large role on several social domains (Chein et al., 2011; Crone & Dahl, 2012; van Hoorn et al., 2016), and social experiences during childhood and adolescence, for example at school, may affect our social decision making to a larger extent than how we are raised by our parents. Therefore, future studies on the development of social learning may benefit from assessing social experiences, social status, and adolescents' social network.

Supplementary materials

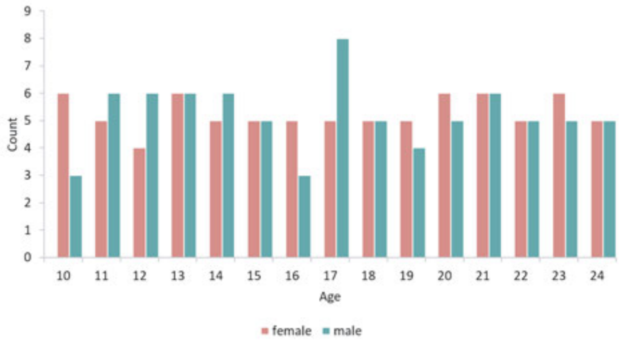


Figure S1. Age and sex distribution across participants of the full sample (N=157). Note that for analyses including parenting effects, we only included participants up to 18 y.o. (N=94).

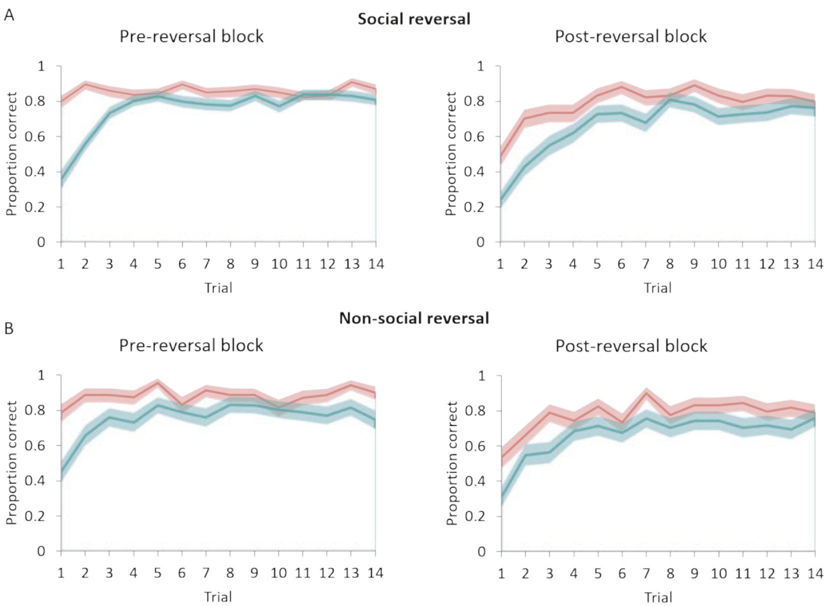


Figure S2. Trust learning performance in the block before and after the reversal. Proportion correct choices over trials per social environment in the pre-reversal block and the post-reversal block. About one half of the participants received a social reversal (shown in panel a), the other half the non-social reversal (panel b). The plots showing the pre-reversal block (left panels) only include data from participants who received the corresponding reversal. Data are pooled across all participants. Over trials, participants adjusted their choices by directing their trust towards players from the Trustworthy environment, and away from players from the Untrustworthy environment.

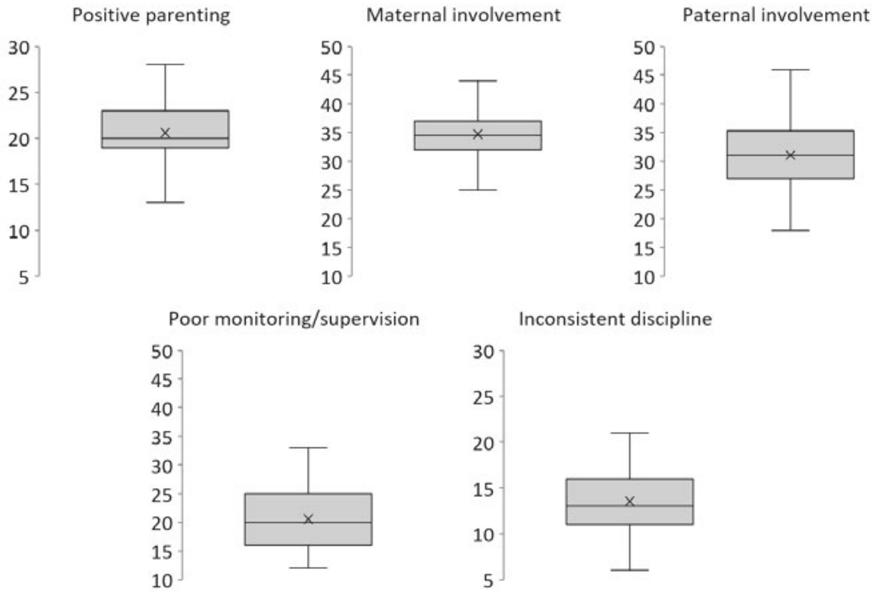


Figure S3. Boxplots for individual differences in parenting subscales. The value range on the y-axis are limited to the possible subscale values.

Supplementary Table 1. Mixed-effects model assessing social and non-social trust learning Results of the binomial generalized linear mixed models (GLMM) testing the effects of Age (linear and quadratic), and all 2-way and 3-way interactions with Environment (Trustworthy vs. Untrustworthy) and Condition (social vs. non-social), on choice behavior (i.e.., “correct” decision) in the trust game. Significant effects are in bold. This GLMM is described fully in the main text.

Predictors	**Main model**					**Main model + sex + IQ**				
	B	*SE*	*Odds Ratios*	*CI*	*p*	*B*	*SE*	*Odds Ratios*	*CI*	*p*
Intercept	1.694	0.077	5.44	4.68 – 6.33	**<.001**	1.693	0.076	5.43	4.68 – 6.31	**<.001**
Age linear	0.312	0.077	1.37	1.18 – 1.59	**<.001**	0.095	0.075	1.38	1.19 – 1.60	**<.001**
Environment	0.408	0.053	1.50	1.36 – 1.67	**<.001**	0.115	0.076	1.50	1.35 – 1.67	**<.001**
Condition	0.057	0.027	1.06	1.00 – 1.12	**.038**	0.323	0.076	1.06	1.00 – 1.12	**.036**
Age quadratic	-0.125	0.076	0.88	0.76 – 1.03	.102	0.408	0.053	0.88	0.76 – 1.02	.093
Age linear * Environment	-0.009	0.053	0.99	0.89 – 1.10	.870	0.057	0.027	0.99	0.89 – 1.10	.879
Age linear * Condition	0.025	0.027	1.03	0.97 – 1.08	.350	-0.127	0.076	1.03	0.97 – 1.08	.343
Environment * Condition	-0.008	0.022	0.99	0.95 – 1.04	.724	-0.008	0.053	0.99	0.95 – 1.04	.724
Environment * Age quadratic	-0.075	0.053	0.93	0.84 – 1.03	.157	0.026	0.027	0.93	0.84 – 1.03	.160
Condition * Age quadratic	-0.009	0.027	0.99	0.94 – 1.04	.728	-0.008	0.022	0.99	0.94 – 1.04	.720
Age linear * Environment * Condition	0.038	0.021	1.04	1.00 – 1.08	.076	-0.074	0.053	1.04	1.00 – 1.08	.077
Environment * Condition * Age quadratic	0.017	0.021	1.02	0.98 – 1.06	.422	-0.010	0.027	1.02	0.98 – 1.06	.428
Sex						0.038	0.021	1.10	0.95 – 1.28	.207
IQ						0.017	0.021	1.12	0.97 – 1.30	.127

Supplementary Table 1. *Continued*

Predictors	**Main model**	**Main model + sex + IQ**
Random Effects		
σ^2	3.29	3.29
τ_{00}	0.83 $_{subject}$	0.82 $_{subject}$
τ_{11}	0.04 $_{subject.Condition}$	0.04 $_{subject.Condition}$
	0.35 $_{subject.Environment}$	0.35 $_{subject.Environment}$
ρ_{01}	0.21	0.23
	0.11	0.1
ICC	0.27	0.27
N	157 $_{subject}$	157 $_{subject}$
Observations	17367	17367
Marginal R^2 / Conditional R^2	0.060 / 0.316	0.064 / 0.316

Supplementary Table 2. Mixed-effects model assessing reversal trust learning Results of the binomial GLMM testing the effects of Age (linear and quadratic), and all 2-way and 3-way interactions with Environment (Trustworthy which was Untrustworthy before the reversal vs. Untrustworthy which was Trustworthy before the reversal) and Condition (social vs. non-social), on choice behavior (i.e.., “correct” decision) in the block after the reversal in the trust game. Significant effects are in bold. This GLMM is described fully in the main text.

Predictors	**Main reversal model**					**Main reversal model + performance in pre-reversal block (2nd half)**				
	B	*SE*	*Odds Ratios*	*CI*	*p*	*B*	*SE*	*Odds Ratios*	*CI*	*p*
(Intercept)	1.236	0.084	3.44	2.92 – 4.06	**<.001**	1.229	0.071	3.42	2.97 – 3.92	**<.001**
Age linear	0.186	0.084	1.20	1.02 – 1.42	**.027**	0.032	0.073	1.03	0.89 – 1.19	.663
Environment	0.403	0.071	1.50	1.30 – 1.72	**<.001**	0.398	0.070	1.49	1.30 – 1.71	**<.001**
Condition	-0.036	0.084	0.96	0.82 – 1.14	.669	-0.032	0.071	0.97	0.84 – 1.11	.647
Age quadratic	-0.013	0.085	0.99	0.84 – 1.16	.874	0.078	0.072	1.08	0.94 – 1.24	.280
Age linear * Environment	-0.139	0.071	0.87	0.76 – 1.00	**.049**	-0.139	0.071	0.87	0.76 – 1.00	**.050**
Age linear * Condition	-0.093	0.084	0.91	0.77 – 1.07	.268	-0.059	0.071	0.94	0.82 – 1.08	.406
Environment * Condition	-0.042	0.071	0.96	0.83 – 1.10	.551	-0.042	0.070	0.96	0.84 – 1.10	.553
Environment * Age quadratic	0.037	0.071	1.04	0.90 – 1.19	.606	0.041	0.071	1.04	0.91 – 1.20	.558
Condition * Age quadratic	0.083	0.085	1.09	0.92 – 1.28	.326	0.073	0.071	1.08	0.94 – 1.24	.305
Age linear * Environment * Condition	-0.061	0.071	0.94	0.82 – 1.08	.390	-0.061	0.071	0.94	0.82 – 1.08	.391
Environment * Condition * Age quadratic	0.021	0.071	1.02	0.89 – 1.17	.766	0.019	0.071	1.02	0.89 – 1.17	.792
Performance pre-reversal block (2nd half)						0.584	0.072	1.79	1.56 – 2.06	**<.001**
Random Effects										
σ^2	3.29					3.29				
τ_{00}	0.84 $_{subject}$					0.51 $_{subject}$				
τ_{11}	0.51 $_{subject.Environment}$					0.51 $_{subject.Environment}$				
ρ_{01}	0.14 $_{subject}$					0.13 $_{subject}$				
ICC	0.29					0.24				
N	155 $_{subject}$					155 $_{subject}$				
Observations	4314					4314				
Marginal R^2 / Conditional R^2	0.050 / 0.326					0.113 / 0.322				

Supplementary Table 3. Mixed-effects models with IQ and sex effects in reversal trust learning

Predictors	**Main reversal model + sex + IQ**				
	B	*SE*	*Odds Ratios*	*CI*	*p*
(Intercept)	1.235	0.084	3.44	2.92 – 4.05	**<.001**
Sex	0.096	0.084	1.1	0.93 – 1.30	.254
IQ	0.053	0.085	1.05	0.89 – 1.25	.534
Age linear	0.187	0.085	1.21	1.02 – 1.42	**.027**
Environment	0.404	0.071	1.50	1.30 – 1.72	**<.001**
Condition	-0.032	0.084	0.97	0.82 – 1.14	.701
Age quadratic	-0.013	0.084	0.99	0.84 – 1.16	.875
Age linear * Environment	-0.139	0.071	0.87	0.76 – 1.00	**.050**
Age linear * Condition	-0.092	0.084	0.91	0.77 – 1.08	.274
Environment * Condition	-0.043	0.071	0.96	0.83 – 1.10	.545
Environment * Age quadratic	0.038	0.071	1.04	0.90 – 1.19	.596
Condition * Age quadratic	0.083	0.084	1.09	0.92 – 1.28	.327
Age linear * Environment * Condition	-0.061	0.071	0.94	0.82 – 1.08	.387
Environment * Condition * Age quadratic	0.021	0.071	1.02	0.89 – 1.17	.765
Random Effects					
σ^2	3.29				
τ_{00}	0.83 $_{subject}$				
τ_{11}	0.51 $_{subject.Environment}$				
ρ_{01}	0.15 $_{subject}$				
ICC	0.29				
N	155 $_{subject}$				
Observations	4314				
Marginal R^2 / Conditional R^2	0.052 / 0.326				

Supplementary Table 4. Mixed-effects model assessing effects of individual differences in parenting on social and non-social trust learning Significant effects are in bold. This GLMM is described fully in the main text.

Predictors	**Main model + parenting (10-18 y.o.)**				
	B	*SE*	*Odds Ratios*	*CI*	*p*
Intercept	1.451	0.094	4.27	3.54 – 5.13	**<.001**
Age linear	0.348	0.117	1.42	1.13 – 1.78	**.003**
Environment	0.460	0.056	1.58	1.42 – 1.77	**<.001**
Condition	0.048	0.034	1.05	0.98 – 1.12	.159

Supplementary Table 4. *Continued*

Predictors	Main model + parenting (10-18 y.o.)				
	B	*SE*	*Odds Ratios*	*CI*	*p*
Positive Parenting	-0.048	0.114	0.95	0.76 – 1.19	.672
Poor Monitoring	-0.163	0.128	0.85	0.66 – 1.09	.204
Inconsistent Discipline	0.003	0.100	1.00	0.82 – 1.22	.973
Involvement Mother	-0.047	0.126	0.95	0.75 – 1.22	.709
Involvement Father	0.096	0.124	1.10	0.86 – 1.40	.439
Age linear * Environment	0.219	0.069	1.24	1.09 – 1.43	**.002**
Age linear * Condition	0.005	0.043	1.00	0.92 – 1.09	.910
Environment * Condition	-0.045	0.026	0.96	0.91 – 1.01	.085
Environment * Positive Parenting	0.003	0.067	1.00	0.88 – 1.14	.966
Condition * Positive Parenting	0.018	0.041	1.02	0.94 – 1.10	.668
Environment * Poor Monitoring	-0.140	0.075	0.87	0.75 – 1.01	.061
Condition * Poor Monitoring	0.003	0.045	1.00	0.92 – 1.10	.949
Environment * Inconsistent Discipline	0.047	0.059	1.05	0.93 – 1.18	.420
Condition * Inconsistent Discipline	-0.005	0.036	0.99	0.93 – 1.07	.885
Environment * Involvement Mother	0.098	0.073	1.10	0.96 – 1.27	.180
Condition * Involvement Mother	-0.031	0.043	0.97	0.89 – 1.06	.478
Environment * Involvement Father	-0.135	0.072	0.87	0.76 – 1.01	.061
Condition * Involvement Father	0.010	0.043	1.01	0.93 – 1.10	.809
Age linear * Environment * Condition	-0.014	0.033	0.99	0.92 – 1.05	.679
Environment * Condition * Positive Parenting	-0.012	0.032	0.99	0.93 – 1.05	.703
Environment * Condition * Poor Monitoring	-0.015	0.034	0.99	0.92 – 1.05	.663
Environment * Condition * Inconsistent Discipline	0.047	0.028	1.05	0.99 – 1.11	.086
Environment * Condition * Involvement Mother	-0.038	0.032	0.96	0.90 – 1.03	.235
Environment * Condition * Involvement Father	0.048	0.033	1.05	0.98 – 1.12	.147
Random Effects					
σ^2	3.29				
τ_{00}	0.76 $_{subject}$				
τ_{11}	0.04 $_{subject.Condition}$				
	0.21 $_{subject.Environment}$				
ρ_{01}	0.59				
	0.09				
ICC	0.24				
N	94 $_{subject}$				
Observations	10371				
Marginal R^2 / Conditional R^2	0.076 / 0.294				

Supplementary Table 5. Mixed-effects model assessing effects of individual differences in parenting on reversal trust learning Significant effects are in bold. This GLMM is described fully in the main text.

Predictors	**Reversal model + parenting (10-18 y.o.)**				
	B	*SE*	*Odds Ratios*	*CI*	*p*
Intercept	1.416	0.200	4.12	2.78 – 6.10	**<.001**
Age linear	0.436	0.235	1.55	0.98 – 2.45	.064
Environment	0.593	0.163	1.81	1.31 – 2.49	**<.001**
Condition	-0.030	0.200	0.97	0.66 – 1.44	.881
Positive Parenting	0.075	0.149	1.08	0.81 – 1.44	.615
Poor Monitoring	-0.225	0.154	0.80	0.59 – 1.08	.145
Inconsistent Discipline	0.016	0.119	1.02	0.80 – 1.28	.895
Involvement Mother	-0.082	0.162	0.92	0.67 – 1.27	.612
Involvement Father	-0.018	0.159	0.98	0.72 – 1.34	.909
Age linear * Environment	0.120	0.191	1.13	0.78 – 1.64	.530
Age linear * Condition	-0.163	0.235	0.85	0.54 – 1.35	.488
Environment * Condition	0.008	0.163	1.01	0.73 – 1.39	.962
Environment * Positive Parenting	-0.003	0.121	1.00	0.79 – 1.26	.977
Condition * Positive Parenting	0.029	0.149	1.03	0.77 – 1.38	.844
Environment * Poor Monitoring	-0.285	0.125	0.75	0.59 – 0.96	**.023**
Condition * Poor Monitoring	0.059	0.154	1.06	0.78 – 1.44	.701
Environment * Inconsistent Discipline	-0.020	0.097	0.98	0.81 – 1.19	.838
Condition * Inconsistent Discipline	-0.022	0.119	0.98	0.77 – 1.24	.851
Environment * Involvement Mother	0.119	0.131	1.13	0.87 – 1.46	.362
Condition * Involvement Mother	-0.013	0.162	0.99	0.72 – 1.36	.937
Environment * Involvement Father	-0.118	0.128	0.89	0.69 – 1.14	.355
Condition * Involvement Father	0.072	0.159	1.07	0.79 – 1.47	.650
Age linear * Environment * Condition	-0.002	0.191	1.00	0.69 – 1.45	.991
Environment * Condition * Positive Parenting	-0.166	0.121	0.85	0.67 – 1.07	.169
Environment * Condition * Poor Monitoring	-0.067	0.125	0.94	0.73 – 1.20	.594
Environment * Condition * Inconsistent Discipline	0.005	0.097	1.00	0.83 – 1.21	.963
Environment * Condition * Involvement Mother	-0.146	0.131	0.86	0.67 – 1.12	.264
Environment * Condition * Involvement Father	0.179	0.128	1.20	0.93 – 1.54	.161
Random Effects					
σ^2	3.29				
τ_{00}	0.88 $_{subject}$				
τ_{11}	0.49 $_{subject.Environment}$				
ρ_{01}	0.02 $_{subject}$				
ICC	0.29				
N	93 $_{subject}$				
Observations	2583				
Marginal R^2 / Conditional R^2	0.093 / 0.359				

3

Supplementary Table 5. Intercorrelations of individual differences in parenting subscales

Spearman correlations	Poor monitoring / supervision	Inconsistent discipline	Maternal involvement	Paternal involvement
Positive parenting	**-.306****	-.027	**.563****	**.516****
Poor monitoring /supervision		**.266****	**-.383****	**-.313****
Inconsistent discipline			-.140	-.017
Maternal involvement				**.650****

*Note: ** = p < .01 (2-tailed). Significant effects in bold.*

Supplementary Table 6. Correlations between age and parenting subscales in subjects up to 18 years

	Positive parenting	Poor monitoring /supervision	Inconsistent discipline	Maternal involvement	Paternal involvement
Age	*rs = -.120* *p = .211*	***rs = .591*** ***p > .001***	*rs = .044* *p = .644*	***r = -.209*** ***p = .028***	*rs = -.168* *p = .077*

Note: Significant effects in bold.

4

Chapter 4

Uncertainty about others' trustworthiness increases during adolescence and guides social information sampling

This chapter is based on (manuscript under review):
Ma, I., Westhoff, B., & van Duijvenvoorde, A. C. K. Uncertainty about others' trustworthiness increases during adolescence and guides social information sampling.

Abstract

Adolescence is a key life phase for developing well-adjusted social behavior. An essential component of well-adjusted social behavior is the ability to update our beliefs about the trustworthiness of others based on gathered information. Here, we examined how adolescents (*N* = 157, 10-24 years) sequentially sampled information about the trustworthiness of peers and how they used this information to update their beliefs about others' trustworthiness. Our Bayesian computational modeling approach revealed an adolescence-emergent increase in uncertainty of prior beliefs about others' trustworthiness. As a consequence, early to mid-adolescents (ages 10-16) gradually relied less on their prior beliefs and more on the gathered evidence when deciding to sample more information, and when deciding to trust. We propose that these age-related differences could be adaptive to the rapidly changing social environment of early and mid-adolescents. Together, these findings contribute to the understanding of adolescent social development by revealing adolescent-emergent flexibility in prior beliefs about others that drives adolescents' information sampling and trust decisions.

Introduction

Adolescence is a life-phase accompanied by a strong social reorientation (Nelson et al., 2016). Adolescents spend more time with peers (De Goede et al., 2009; Lam et al., 2014; Larson et al., 1996), are susceptible to peer influence (Albert et al., 2013; Gardner & Steinberg, 2005), and aim to achieve and maintain a positive peer status (Crone & Dahl, 2012; Gavin & Furman, 1989; LaFontana & Cillessen, 2010; Nelson et al., 2016; Steinberg & Silverberg, 1986). Violations of trust, such as social rejection, gossiping, and other negative peer interactions are exceptionally detrimental to adolescents' mental health and social development (Blakemore, 2008; Crone & Dahl, 2012). It is therefore imperative for adolescents to sample information about the trustworthiness of their peers to update their beliefs and adapt their behavior accordingly. For example, information can be sampled by asking close friends for their opinion about a specific peer or by observing how they treat others. When the sampled information indicates that the peer violates the trust of others, the adolescent should update their belief about that peer's trustworthiness (from likely trustworthy to likely untrustworthy) and adapt their behavior towards that peer accordingly.

However, sparse samples might not be representative of the peer's true trustworthiness. An untrustworthy peer might sometimes act in a trustworthy manner. Insufficient information can therefore result in erroneously trusting an untrustworthy peer or not trusting a trustworthy peer. Despite the relevance of trustworthiness information sampling to the social development during adolescence, not much is known about the age differences that take place in this process. Understanding how adolescents determine the quantity of their trustworthiness information samples, sheds light on the adaptive changes that underlie social development and may expose potential improvements.

From a social reorientation perspective, it might be intuitive to expect that adolescents focus more on peers and therefore excessively sample information about peers compared to children or adults. However, a recent study using a novel task and computational model identified three distinct factors that underlie the process of information sampling about others' trustworthiness in adults (Ma, Sanfey, et al., 2020) giving rise to more nuanced hypotheses about information sampling in adolescents. The main factors that were identified in the study were: 1. prior beliefs about trustworthiness, 2. uncertainty about the prior belief, and 3. uncertainty tolerance. The first factor, the *prior beliefs about trustworthiness*, is an individual's initial expectations about others' trustworthiness before any information is sampled. Past studies in adults show that biased prior beliefs subsequently biases how information is sampled and how the beliefs are updated in the light of new information (Chang et al., 2010; Fareri et al., 2012). For example, adults were more likely to update their beliefs about another person if the novel information was consistent with their prior beliefs (Fareri et al., 2012), and actively sample information to support their prior beliefs (Kaanders et al., 2021). Prior beliefs about trustworthiness might show age differences across adolescence. Empirical studies have shown that initially placed trust increases from childhood to adulthood (Fett, Shergill, et al., 2014; Sutter & Kocher, 2007; van den Bos et al., 2010, 2011), suggesting a potential shift in prior beliefs about trustworthiness during adolescence (but see Flanagan & Stout, 2010). One of the aims of the current study is therefore to assess if prior beliefs about trustworthiness indeed shift during adolescence and affects information sampling or bias decisions to trust or not trust a peer.

The second important factor when sampling information is the *uncertainty about prior beliefs* (Ma, Sanfey, et al., 2020). This reflects the variation an individual expects in the trustworthiness of others. We first explain this concept in more detail before discussing potential changes during adolescence. For example, an individual with high uncertainty about their prior belief expects more variation in trustworthiness between different trustees. In contrast, an individual with low uncertainty about their prior belief expects that there will be little variation in trustworthiness between different trustees. There can be uncertainty about any prior belief; one individual might expect that all trustees are untrustworthy (low uncertainty), another could expect that everyone is trustworthy (low uncertainty), and yet another might expect that some are trustworthy while others are not (high uncertainty). Each new sample updates both the belief and the uncertainty. The updated result is a posterior belief and uncertainty about the posterior belief, respectively. Adults were shown to sample information until their posterior uncertainty dropped below a level to which they were tolerant to uncertainty (Ma, Sanfey, et al., 2020). Uncertainty about prior (and posterior) beliefs thereby influence the quantity of information samples, such that higher uncertainty likely result in more sampling (Ma, Sanfey, et al., 2020).

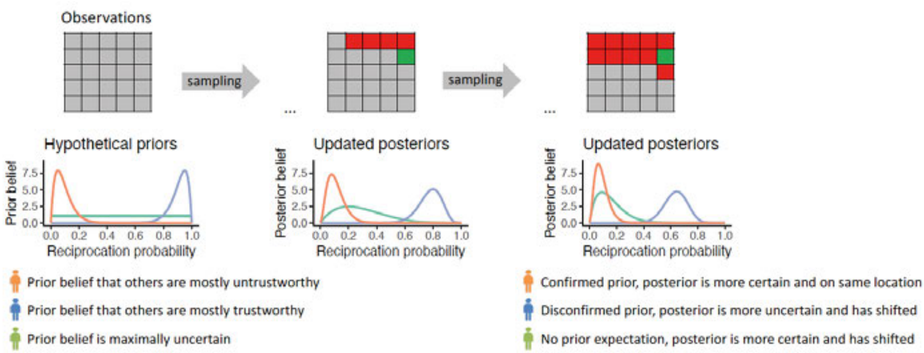


Figure 1. Illustration of how prior belief distributions update to posterior beliefs. The grid represents sampled information about trustworthiness. A green tile indicates that the sample resulted in an observation of trustworthiness, red tiles represent observations of untrustworthiness, and grey tiles are not sampled. At the start all tiles are grey as no samples have been drawn yet and therefore the current

belief distribution about trustworthiness is the prior belief distribution. The belief updates with each sample. The updated posteriors in the middle reflect an intermediate belief stage when there are 4 red and 1 green tile. The orange, green and blue lines in the plots represent three hypothetical subjects' prior distributions and their corresponding posterior distribution. These three hypothetical subjects were selected to show that the posterior beliefs can be quite different depending on the prior expectation (mean) and the prior uncertainty (variance) of the prior belief distribution. The orange prior distribution reflects the expectation that lower reciprocation probabilities are more likely. The observed outcomes exactly match that prior expectation. The posterior uncertainty therefore decreases but the posterior mean does not update. The blue prior distribution reflects a belief that higher reciprocation probabilities are more likely. The sample outcomes disconfirm this belief and the posterior therefore shows a large update and becomes more uncertain. The green prior distribution has a maximal uncertainty, i.e., a belief that all reciprocation probabilities are equally likely. The posterior then shows a both large update in the mean and a reduced uncertainty.

Little is known about the development of uncertainty about prior beliefs during adolescence, possibly because beliefs and especially uncertainty are difficult to observe directly in choice behavior and often require assessment through Bayesian computational models. Uncertainty about prior beliefs of trustworthiness likely change during adolescence, as changes take place in the set and frequency of social behaviors displayed by peers during early adolescence (e.g., courtship or competitive behavior such as gossiping). Transitioning from primary to high school exposes the adolescent to new peer groups with new group dynamics. Normatively, this novelty in the social environment should increase uncertainty about the generalizability of previously learned social behaviors (Piray & Daw, 2020; Stamps & Frankenhuis, 2016) (e.g., "childish" games such as playing tag may not be socially accepted anymore in high school). Specifically, uncertainty about prior beliefs should *increase* when the environment becomes more volatile, which leads to heightened sensitivity to new information, thereby allowing the individual to update their beliefs more with each new information sample (Behrens et al., 2007). Given the numerous changes in adolescents' social lives, we therefore expect an age-related *increase* in their uncertainty about their prior beliefs of peers' trustworthiness.

The third and final factor is *uncertainty tolerance*, which reflects the level of posterior uncertainty that an individual finds tolerable (Ma, Sanfey, et al., 2020). As mentioned earlier, this affects the sample quantity together with the uncertainty about prior beliefs, as adults sample until their posterior uncertainty drops below their uncertainty tolerance level (Ma, Sanfey, et al., 2020). Previous developmental studies showed individual and age-related differences in how tolerant adolescents are to uncertainty by using questionnaires (Boelen et al., 2010; Dekkers et al., 2017) and experimental risky choice tasks that vary the level of outcome uncertainty (Dekkers et al., 2017). In general, these studies with experimental tasks suggest that adolescents are more tolerant to uncertainty, which led them to explore risky gambles more often, compared to adults (Blankenstein et al., 2016; Tymula et al., 2012) (but see Blankenstein et al., 2018; Braams et al., 2019). One previous study explored how uncertainty tolerance related to sampling information for monetary rewards. Findings showed that adolescents sample less information about lottery outcomes than children and adults, also suggesting that adolescents are more uncertainty tolerant than children and adults (Van Den Bos & Hertwig, 2017). Whereas these previous studies suggest that uncertainty tolerance is a trait that underlies risky choice, little is known about how an individual's level of uncertainty tolerance drives behavior in the social domain in adolescence. Given that information about peers is highly important for adolescents to successfully navigate their changing social environment, adolescents' uncertainty tolerance in non-social lottery tasks might not generalize to sampling information about peers and instead adolescents might become more uncertainty intolerant with age, especially from early to mid-adolescence.

In summary, here we examined how age differences in prior beliefs about trustworthiness, uncertainty about prior beliefs about trustworthiness, and uncertainty tolerance as factors that potentially may affect age-related differences in information sampling about others' trustworthiness. Participants (10-24 years, *N* = 157, 75 of which were boys) completed the Information Sampling Trust Game (ISTG, see Figure 2A). The Trust Game mimics characteristic consequences of trust, such that trusting is beneficial to all involved partners if reciprocated, but trust can also be betrayed. The ISTG extends this paradigm by allowing the participant to sample information about the trustee's history of trustworthiness prior to making a decision to trust or not trust.

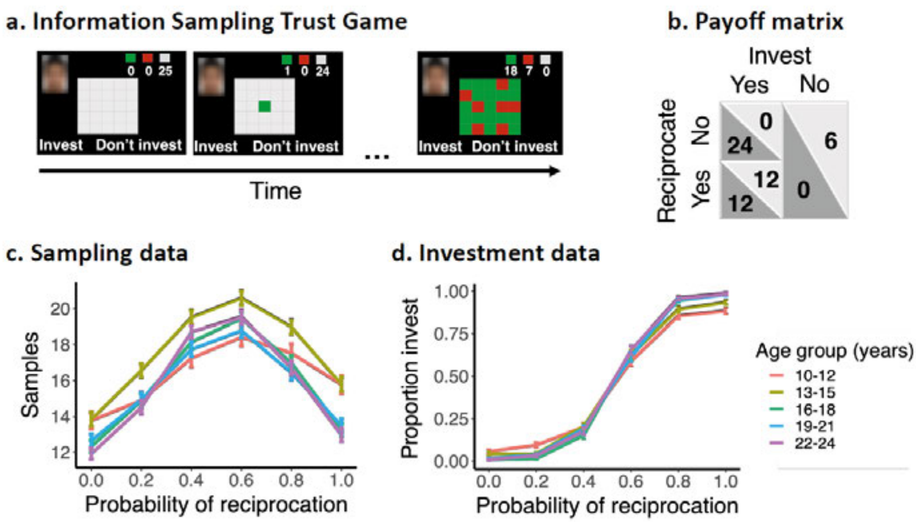


Figure 2. Information Sampling Trust Game and data. **(A)** Task trial sequence example and payoff matrix. On each trial there are 2 players: the investor and a trustee. The participants played in the investor role and could sample a trustee's reciprocation history with other investors up to 25 times by turning tiles in a 5 by 5 grid. Green = reciprocated trust, red = betrayed trust, grey = not sampled. Investment

outcomes were not shown during the task. Six reciprocation probability conditions (r = 0.0, 0.2, 0.4, 0.6, 0.8, 1.0) generated the outcomes in the grid. It was clarified that they were playing with someone their own age, that the location of the tile was not informative, that each trial would be played with a new unknown trustee, and that the ratio green to red tiles would thus vary between trials. **(B)** Payoff matrix. Participants were told that if they invested, the trustee received the 6 tokens, which would be multiplied by 4 (24 tokens) and subsequently the trustee decided to either reciprocate by splitting the 24 tokens 50-50, or defect and keep all 24 tokens to themselves. Participants also had the option of not investing by keeping the initial endowment. **(C)** The number of samples (mean and standard error of the mean (s.e.m.)) as a function of reciprocation probability per age group (years). Age groups were created for visualization purposes only and analyses were conducted with age as continuous measure. **(D)** Proportion of investments as function of the generative reciprocation probability for each age group.

At the beginning of each trial, participants were endowed with 6 tokens which they could invest (entrust) in the trustee in a single-shot Trust Game (see Figure 2B for payoff matrix). Participants were told that these trustees previously played this game with 25 different investors in a different experiment and that their decisions to reciprocate or defect were stored in a covered 5 x 5 grid. Participants were given the opportunity to first sample information about the trustee's reciprocation history before deciding to either invest or not invest. Unbeknownst to participants, the grid outcomes were computer-generated and drawn from the following probabilities: 0.0, 0.2, 0.4, 0.6, 0.8, and 1.0, where 0.0 is completely untrustworthy (all red) and 1.0 is fully trustworthy (all green). Each subject sampled information about 60 different trustees (trials). There were no explicit sampling costs other than the time and effort involved in turning tiles. The outcomes of participants' trust decisions (invest or not invest) after sampling were not shown during the task to avoid changing meta-beliefs about the reliability of the acquired information. Instead, participants were told that 3 trials would be randomly selected at the end of the task and their average amount of tokens would be converted to money and paid to the participant (see Supplementary materials).

Results

Descriptive statistics

On average participants sampled 16.229 (SD = 7.532) of 25 times per trial. We expected based on non-social sampling studies (Fiedler & Juslin, 2006) that participants would sample more when the sample outcomes were less consistently green or red (i.e., when the outcome uncertainty was highest) and we examined the interaction with age. To this end we used a linear mixed effects model (LME4 in R (Bates et al., 2014; R Core Team, 2020) assessing the effects of outcome uncertainty (i.e., the variance in the Bernoulli distribution r (1-r) where r is the probability of reciprocation) and the linear and nonlinear age effects (polynomial models of linear and quadratic age effects) on the number of samples. In all our analyses, we report the best fitting mixed-effects model results (see Supplementary materials for the full mixed effects model specification).

We found that participants sampled significantly more when the outcome uncertainty was higher, i.e., when the probability of reciprocation was closer to 0.5 (B = 2.103, p < .001, see Figure 2C). This effect interacted with the linear effect of age (B = 0.416, p < .001). There was no significant main effect of age (B = -0.467, p = .278). We conducted post-hoc Bonferroni-holm corrected analyses to further examine the interaction effect with age. This showed that the effect of outcome uncertainty was significantly less strong in early-adolescents while older age groups did not significantly differ from each other (see Supplementary materials for R code and all pairwise comparisons). Moreover, the effect of age on the number of samples was significantly stronger when the trustee was highly trustworthy (i.e., when the probability of reciprocation was closer 1.0) and when the trustee was highly untrustworthy (i.e., when the probability of reciprocation was closer to 0.0). This suggests that participants sampled less with age when trustees were very trustworthy or untrustworthy, (see Figure 2C).

Next, we used a mixed-effects model to examine whether the invest decisions (i.e., decisions to trust or not) were predicted by trustworthiness (i.e., the reciprocation probability) and whether this differed with age. As expected, we found a significant main effect of trustworthiness (β = 3.414, p <0.001), showing that the likelihood of investing increased when the trustee was more trustworthy. There was a significant interaction between trustworthiness and the linear effect of age (β = 0.860 , p < .001). Post-hoc linear mixed models per reciprocation probability were done to further examine the interaction with age. This showed that adolescents were more likely to invest in highly trustworthy trustees with age (reciprocation probability 0.8, B = 0.044, p < .001; reciprocation probability 1.0, B = 0.040, p < .001) and more likely to not invest in highly untrustworthy trustees (when the probability of reciprocation was 0.0, B = -0.020, p = .001, also see Supplementary materials for all results). Taken together, this suggests that younger participants were less likely to trust peers who were trustworthy and to some extent more likely to trust untrustworthy trustees compared to older adolescents, even though younger adolescents sampled more information about trustworthy peers than older participants (see Figure 2C and 2D).

Computational processes underlying trustworthiness information sampling

Information sampling and age differences therein were well captured by a Bayesian model of information sampling, called the Uncertainty model (Ma, Sanfey, et al., 2020). At its core, this model has a Bayesian belief distribution over the trustworthiness of the trustee. This belief distribution encompasses the prior belief and the uncertainty about the prior belief. With each sample this belief distribution is updated, resulting in the posterior belief distribution. The probability of stopping the information sampling increases as the updated uncertainty drops below the uncertainty tolerance level (see Methods for formal description).

We compared the Uncertainty model against three alternative computational models to test if trustworthiness information sampling strategies differed with age (see Methods for formal descriptions). The Sample Cost model and the Threshold model are alternative models developed in a previous study on the ISTG (Ma, Sanfey, et al., 2020) and the Count model was added to test if a simpler heuristic strategy is more prevalent in late childhood than at older ages. The *Sample Cost model* uses the Bayesian belief distribution to compute the normative solution for every state. The *Threshold model* is similar to the Uncertainty model without using a Bayesian beliefs distribution but instead it is based on the concept of sampling until the ratio between red and green tiles meets a subjective threshold. Finally, the *Count model* is the simplest model and tests if participants are insensitive to the gathered evidence and instead sample a fixed number of tiles with some variation.

The Uncertainty model fitted better than these alternative models for all ages (see Figure 3A), replicating previous findings in adults (Ma, Sanfey, et al., 2020). We assessed significance of the model fit difference by using bootstrapping to compute the 95% CI's of the BIC differences (see Figure 3B). This showed that the Uncertainty model fitted significantly better than all other models (95%CI of the summed BIC difference between the Uncertainty model and the Sample cost model was 95%CI [-3086, -527], the difference from the Threshold model was 95%CI [-3072, -636], and from the Count model 95%CI [-55095, -48774], see Figure 3B). We also performed Variational Bayesian Analyses (Rigoux et al., 2014) which returned a high probability that the Uncertainty model was most frequent in the comparison set (protected exceedance probability: Uncertainty model = 0.994, Threshold model = 0.005, Sample Cost model = 0.051, Count model = 0.000). Importantly, the Variational Bayesian Analyses for group comparisons returned a high probability that the five age groups have the same winning model (p(same winning model) = .907, see Figure 3C for model fit per age bin). We verified through model recovery that the models were distinguishable and through parameter recovery that the number of trials was sufficient to accurately estimate parameters (see Supplementary materials).

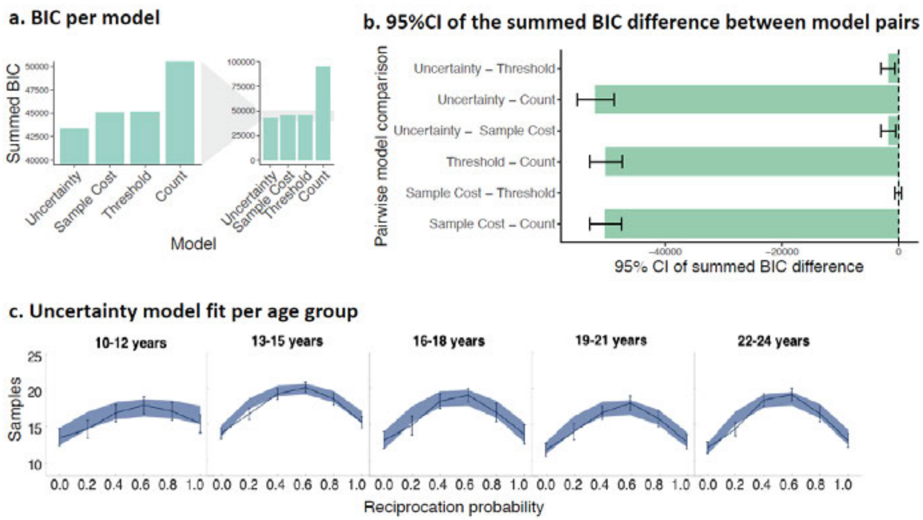


Figure 3. Model fit results. **(A)** The Bayesian Information Criterion (BIC) per model summed over participants. Lower BIC values indicate a better fit, thus showing that the Uncertainty model fits best. BIC scores were computed for each participant and each model. Left image is zoomed in as the count model fitted much less well than the other models. Right image is not zoomed in. The grey area shows the zoom range. **(B)** 95% confidence intervals (CI) of the summed BIC difference between models. Zero indicates no difference between models. Negative values are in favor of the model before the subtraction sign, as lower BIC indicates a better fit. The Uncertainty model fits significantly better than the Sample Cost and Threshold models (95% CI does not contain zero). The BIC scores of a model pair were subtracted from each other for each participant, thereby obtaining one difference score per participant for each model pair. To assess significance, the 95% confidence interval of the BIC difference was computed using bootstrapping with 10^5 iterations. **(C)** Uncertainty model fit across age. Age is grouped for visualization purposes. The shaded area is the s.e.m. of the data that was simulated with the participants' estimated parameters in the Uncertainty model. The line graph represents the mean and s.e.m. of the participants' actual data. The overlap between the shaded area and line graphs show that the Uncertainty model fitted well for each age group.

Prior beliefs, prior belief uncertainty, and uncertainty tolerance underlie age-related differences in trustworthiness information sampling

Given our expected age-differences in prior beliefs, prior belief uncertainty, and uncertainty tolerance, we examined linear and non-linear effects of age on these model derived metrics using linear regression models. For each metric, we compared linear, polynomial (linear and quadratic), and logarithmic age effects and report the best fitting regression model results. We found that the *prior beliefs* increased monotonically with age (age linear, $\beta = 0.212$, $p = .009$). Though this effect was subtle, it shows that with age, participants expected peers to be more trustworthy (see Figure 4). Interestingly, the *prior belief uncertainty* strongly increased from early to mid-adolescence (ages 10-17 years) and then stabilized (Figure 4). The best fitting age-model was polynomial, showing a significant linear (β = 0.49, p < .001) and quadratic effect of age (β = -0.43, p = .010). This suggest an adolescent-emergent increase in uncertainty about their prior beliefs of trustworthiness. Moreover, *Uncertainty tolerance* increased linearly with age (β = 1.80, p < .001, Figure 4), suggesting that adolescents gradually became more uncertainty tolerant with age. Finally, *decision noise* did not change with age (linear, β = -0.12, p = .587, quadratic, β = 0.38, p = .119). This shows that the degree to which participants' sampling choices followed the fitted Uncertainty model predictions did not change with age and therefore gives more confidence in the interpretability of the model derived metrics across adolescence.

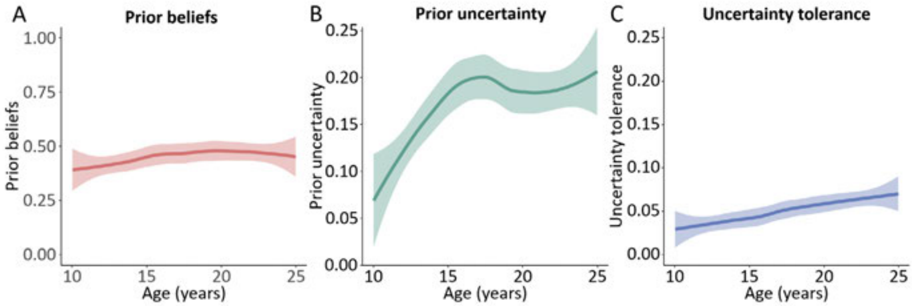


Figure 4. Prior beliefs, prior uncertainty, and uncertainty tolerance as function of age. Note that a uniform prior corresponds to a prior uncertainty of 0.289, which is the width of the beta distribution for uniform priors. This thereby creates an upper bound for the prior uncertainty. Uncertainty tolerance has the same upper bound as prior uncertainty, as they both reflect the width of the belief distribution. Lower prior uncertainty values reflect a more certain prior. The Loess method was used to generate these plots.

No difference in prior beliefs in first and second task-half

To test if the prior beliefs changed during the task, we refitted the Uncertainty model to the first half and second half of the task separately. The prior belief is a model derived metric based on two free parameters in the Uncertainty model, called a_0 and b_0 (see Methods). Since different combinations of a_0 and b_0 can result in the same prior belief (but with different uncertainty about those prior beliefs), we conducted these analyses on the a_0 and b_0 parameter estimates rather than on the prior beliefs. Wilcoxon sign-rank tests showed no difference between the first and second task halves in either of the these two parameter estimates (a_0 estimate, z = 1.406, p = .160, median difference < 0.001, 95% CI [-0.122, 0.315]; b_0 estimate, z = 1.133, p = .257, median difference < 0.001, 95% CI [-0.478, 0.465]). Moreover, Spearman-rank correlations showed no significant relation between age and the difference between the first and second task halves in either of the two parameter estimates (a_0 estimate

r_s = -0.046, p = .565; b_0 estimate r_s = -0.058, p = .573). Since uncertainty about the prior belief was also a metric derived from the a_0 and b_0 parameters (see Methods), this suggests that our findings of the prior beliefs and uncertainty about those beliefs were not likely confounded by changes over trials or age-related changes therein.

Discussion

Gathering information about outcomes of social interactions to adjust our beliefs about others is critical for successful and adaptive social behavior. Sampling and using information about others is particularly important during adolescence, as this is a developmental phase in which social cognition and peer relations rapidly develop. We found that adolescents adjusted their sampling quantity to the consistency of the sampled information by sampling more when the information was inconsistent. This effect of information inconsistency was less strong for early-adolescents compared to older adolescents. Moreover, adolescents trusted (i.e., invested) more often when peers were more trustworthy and this adaptive response to high trustworthiness became stronger with age. These behavioral findings show age differences in social information sampling and its use in trust decisions. The age differences in information sampling were well captured by a computational model in which a Bayesian belief distribution over trustworthiness is updated with each new sample. The computational model showed that the age differences in sampling could be accounted for by age differences in prior beliefs about trustworthiness, uncertainty about those prior beliefs, and uncertainty tolerance.

We found a relation between age and prior beliefs, which indicated that with age, adolescents believed others to be more trustworthy before having sampled any information. This finding is consistent with previous developmental studies that have used (repeated) trust games and found that the first invested amount in the trust game tends to increase with age (Fett, Shergill, et al., 2014; Sutter & Kocher, 2007; van den Bos et al., 2010, 2011), suggesting more initially placed trust in others. Our computational model also showed that the relation between age and prior beliefs accounted for the, albeit subtle, finding that younger adolescents sampled more relative to older adolescents when the underlying reciprocation probabilities were either high or low (Figure 3C). Intuitively, when the sampled information indicated that the trustee was very trustworthy or very untrustworthy, it contradicted the prior beliefs of early-adolescents more than the older adolescents. This resulted in a sampling bias where early-adolescents sampled more relative to older adolescents when the trustee was highly trustworthy or highly untrustworthy, as they needed more information to be convinced of the information. The age-related increase in prior beliefs was subtle, yet possibly adaptive to age-related changes in the trustworthiness of peers, as earlier studies found that adolescents indeed become more trustworthy from early to mid-adolescence (Harbaugh et al., 2003; Sutter & Kocher, 2007).

The strongest and most striking age difference was found in the uncertainty about prior beliefs. Confirming our hypothesis, prior beliefs about others' trustworthiness rapidly became more uncertain with age from early to mid-adolescence. This adolescence-emergent increase in prior uncertainty led adolescents to rely less on their prior beliefs and more on their sampled information. Behaviorally, this resulted in adolescents rapidly adapting their sampling behavior to the information inconsistency from early to mid-adolescence. In other words, early to mid- adolescents became more open-minded about possible individual differences in trustworthiness between peers. The increase in uncertainty about prior beliefs is not likely explained by age-related differences in sampling strategies or task comprehension for at least four reasons. Firstly, we ruled-out alternative computational models that represented alternative sampling strategies, showing that participants of all ages used the same information sampling strategy in their decisions to continue sampling. Second, the instructions were read aloud and in-person by the experimenters who made sure all participants understood the task by asking comprehension questions. Third, age differences in task comprehension cannot account for all age-related effects, such as the relation between age and prior beliefs. Finally, the prior belief distribution parameter estimates did not differ between the first and second task half, which indicates that the age-related increase in prior uncertainty was not due to age differences in sampling strategies or task comprehension as the task progressed.

The increase in uncertainty about prior beliefs may be adaptive given the numerous changes that take place in early to mid-adolescents' social environment, including changes in social behavior induced by the peers' pubertal stage and a transition of schools. Interestingly, given that the changes in the adolescent's environment occur mostly in social contexts but less so in non-social contexts (e.g., physics such as gravity mostly remain constant), this further suggests that learning flexibility in adolescents might be especially strong in social contexts. This pertains to learning about others or about the self in relation to a peer group. Future within-subjects studies are required to examine if the age-related increase in uncertainty about prior beliefs is indeed specific to social contexts, and in which social contexts this may be most pronounced.

We furthermore found that uncertainty tolerance increased linearly with age. This finding at first seems to contradict previous studies on uncertainty tolerance in non-social contexts, which suggest that adolescents are more uncertainty tolerant than adults (Blankenstein et al., 2018; Tymula et al., 2012; Van Den Bos & Hertwig, 2017). However, in the Uncertainty model, uncertainty updates with each sample and the probability to stop sampling increases once uncertainty drops below the individual's uncertainty tolerance level. Therefore, uncertainty tolerance should be interpreted in combination with uncertainty about prior beliefs. In our study, mid-adolescents relative to early-adolescents showed increased uncertainty about prior beliefs combined with a smaller increase in uncertainty tolerance. In the model this combination results in an increase in sampling (see model simulations in Figure 3C). After mid-adolescence, uncertainty about prior beliefs stabilized while uncertainty tolerance continued to increase. In the model, this combination resulted in a decrease in sampling from mid to late-adolescence (Figure 3C). Although we did not test non-social information sampling in this study, the idea of at least some degree of social specificity is corroborated by previous studies on non-social information sampling. Those studies found that adolescents gathered less information than children or early-adolescents prior to a risky financial decision (Bowler et al., 2020; Van Den Bos & Hertwig, 2017), which diverges from our findings in a trust context. Taken together, our findings of age-related differences in the factors that underlie information sampling fit with our notion that mid-adolescents may attempt to learn more about their social environment.

While reinforcement learning studies on adolescence are scarce, one advantage of this computational modeling approach is using formal model comparisons to assess age-related differences in decision-making strategies (Cohen et al., 2020; Kabotyanski et al., 2019; Palminteri et al., 2016). For example, a previous study showed that adolescents used different reinforcement learning strategies than adults by not benefitting from counterfactual feedback, which would have been challenging to conclude without the specific behavioral predictions that result from fitting computational models (Palminteri et al., 2016). In the current study, we ruled-out a family of normative models (i.e., Sample Cost model variants), heuristic models that were not based on Bayesian belief distributions (Threshold model variants), and the Count model for insensitivity to gathered evidence. We found that the Uncertainty model showed a good fit and fitted best for all ages, showing that across age, adolescents use their uncertainty in Bayesian belief distributions to update their beliefs about trustworthiness. This is consistent with a previous study on social information sampling costs in adults, where the Uncertainty model also fitted the data best (Ma, Sanfey, et al., 2020). We show that within this winning model, age-related differences in the parameter estimates accounted well for age differences in sampling behavior. Our computational modeling and model comparison approach therefore contributes to the field's understanding of age differences in cognitive strategies of social decision-making.

The potential applications of our approach extend to understanding how peer-status could influence prior beliefs about others' behavior. For instance, children who are frequently socially rejected by their peers may develop different prior beliefs over the trustworthiness of others compared to stably accepted children (e.g., those with experience of frequent rejection may have a highly certain prior belief that others are untrustworthy). Moreover, previous studies used behavioral economic games such as trust games to reveal aberrant social decision-making in psychiatric disorders (Hinterbuchinger et al., 2018; King-Casas & Chiu, 2012; Robson et al., 2019), including anxiety disorders, autism spectrum disorder (Izuma et al., 2011), borderline personality disorder (King-Casas & Chiu, 2012; Seres et al., 2009; Unoka et al., 2009), and ADHD (Ma et al., 2016, 2017). In future studies, our task and models might further shed light on how individuals actively sample and use information to initiate or avoid social interactions and how this may depend on aberrant prior beliefs.

Methods

Participants and experiment procedure

A total of 157 adolescents (of which 75 boys) completed the experiment (range = 10-24 years, M = 17.50, SD = 4.34). The sample size was based on prior studies examining age-related differences in uncertainty tolerance within a comparable age-range (Blankenstein et al., 2016; Van Den Bos & Hertwig, 2017). Participants were screened for color blindness, psychiatric and neurological disorders, IQ was estimated by using subtests of the WISC and WAIS. IQ scores fell in the normal range (M =107.5, SD = 10.9, range = 80-135), and did not correlate with age (r_s = 0.119, p = .138), parental social economic status (SES) was estimated by highest educational attainment of the caregiver (s). This sample generally showed a medium to high SES level and SES did not show a relationship with age (Kruskal-Wallis rank sum returned χ^2 (4, n = 157) = 6.342, p = .175; low SES n =8, medium SES n = 59, high SES n = 90). All procedures were approved by the institutional review board of the Leiden University Medical Center, and performed in accordance with the relevant guidelines and regulations. Written informed consent was given by adult participants, and by their legal guardians in the case of minors (minors provided written assent). This behavioral study was part of a larger imaging study. All participants performed the task in a quiet room near the neuroimaging labs of Leiden University. The task took approximately 30 minutes to complete (see Supplementary materials for payoff procedure).

Computational model

The Uncertainty model is based on the concept of sampling to reduce uncertainty until the subjective uncertainty tolerance is met. The model consists of four components: a prior belief distribution over the reciprocation probability (r), an evolving posterior distribution over r, the uncertainty tolerance, and decision noise. As explained above, individuals start with a prior belief distribution when nothing has been sampled yet. This prior belief distribution encompasses both the prior belief and the uncertainty about the prior belief. When information is sampled, the belief distribution is updated and called a posterior distribution. The posterior distribution is therefore a combination of the prior belief distribution and the sampled information. Information is sampled sequentially and each new sample results in a new update. The degree to which the prior beliefs and the uncertainty about prior beliefs update with each new sample depends on the values of the prior belief and uncertainty about prior beliefs and whether the prior belief is confirmed or disconfirmed by the samples. Examples of how belief updates depend on prior belief distributions and samples are depicted in Figure 1.

Formally, in our model the *state* is defined by the number of turned green tiles (n_+) and the number of turned red tiles (n_-). The *actions* are to either sample or stop sampling until all 25 tiles are sampled. Specifically, the model assumes that people do not know the trustee's exact trustworthiness by using a Bayesian belief distribution over the possible range of *r*. The conjugate prior belief distribution over *r* is a beta distribution with parameters α_0 and β_0. As information is sampled, the evolving posterior distribution is:

$$p(r|n_+, n_-) = \mathrm{Beta}(r; \alpha, \beta) \tag{1}$$

The Beta distribution consists of parameters α and β. Here, $\alpha = \alpha_0 + n_+$ and $\beta = \beta_0 + n_-$.

As shown in Figure 1, the more uncertain a prior is, the more a new sample will reduce that uncertainty. In addition, if a sample is highly consistent with the prior expectation, the posterior mean will shift less than when a sample disagrees with the belief (Stamps & Frankenhuis, 2016). Uncertainty of the belief is operationalized using the standard deviation of the posterior distribution:

$$\mathrm{Uncertainty}(\alpha, \beta) = \sqrt{\frac{\alpha\beta}{(\alpha+\beta)^2(\alpha+\beta+1)}} \tag{2}$$

As sampling decreases uncertainty and at some point, the uncertainty will reach the subject's uncertainty tolerance *k,* i.e., how much uncertainty is tolerated by the subject. As the uncertainty reduces and approaches the tolerance, the probability that the subject takes another sample becomes smaller. These probabilities are given through the softmax function, allowing for decision noise τ:

$$p(\mathrm{sample}|\alpha, \beta) = \frac{1}{1 + e^{\frac{Uncertainty(\alpha,\beta)-k}{\tau}}} \tag{3}$$

Where a larger *k* reflects more uncertainty tolerance and a larger τ reflects more decision noise.

We fitted the model for each participant individually using a log likelihood optimization algorithm as implemented in the fmincon routine in MATLAB (Mathworks) using 100 combinations of starting points to avoid local minima. Four free parameters are fitted for each subject: α_0, β_0, *k,* and τ. In addition, we used between-subjects Bayesian Model Selection

(Rigoux et al., 2014; Stephan et al., 2009) to assess variation in the best fitting model between different ages using five age groups.

Alternative models

We also considered three families of alternative models and found that these did not fit as well as the Uncertainty model (formal descriptions in Supplementary materials): The *Sample Cost model*, which uses the Bayesian belief distribution to compute the normative solution for every state. The *Threshold model* is a heuristic model that does not use Bayesian beliefs distributions. For model comparisons we calculated the difference between model evidence in terms of BIC for each model pair for each subject. The Count model is the simplest heuristic model. In this model, a fixed number of samples are drawn with some variation. Unlike the other models, the decision or stop sampling is therefore not dependent on the outcomes of previous samples. To assess the significance of the model fit differences, we used bootstrapping to compute the 95% confidence intervals of the summed difference in BIC using 10^5 iterations (for within-model results see Table S1).

Data and code availability

The data of this study are openly available in Open Science Framework osf.io/upmwv and the code is available on Github on request https://github.com/ili-ma/Social_Belief_Updates_Adolescence.

Supplementary materials

Participant recruitment

Participants were recruited through flyers and presentations at local high schools in the Netherlands, as well as a recruitment website. Based on previous studies (see methods section), we aimed to recruit 160 participants equally divided across 5 age bins (10-12; 13-15; 16-18; 19-21; 22-24 years) with a balanced gender distribution for each age bin. Eventually, 159 people came to the laboratory to participate in our study protocol. One person did not start the study due to anxiety. One person could not finish the sampling experimental task due to time constraints. This led to the reported *N* of 157 adolescents.

Participant bonus fee

Unbeknownst to the participants, payoff was not dependent on trustee decisions, instead three trials were selected and their outcome was averaged to determine payoff. If invested and the generative reciprocation probability was > 0.5 then the outcome was 12 tokens, and 0 tokens if < 0.5. To avoid extreme bonus differences between participants, the payoff trial selection procedure was not fully randomized such that each participant ended with a task performance bonus about between 3 and 9 tokens. The tokens were converted to money as follows: 3 = €1, 4 = €2, 5 = €2, 6 = €3, 7 = €3, 8 = €4, and 9 = €5 and this amount was added to the participation fee.

Computational models

Note that for all models, we tested different variants within each model, and selected the best fitting version for between model comparisons. Here, we denote the best fitting version of each model, for all versions see Ma et al., (2018).

The Sample Cost model

The Sample Cost model uses the Bayesian belief distribution over trustworthiness to compute the expected utility of sampling and stopping for every possible state in the task through forward reasoning. It consists of four components: prior beliefs over the trustworthiness (*r*), an evolving posterior distribution over *r* iterative maximization of future expected utility under this posterior distribution, and decision noise. The conjugate prior over *r* is a beta distribution with priors α_0 and β_0, and parameters $\alpha = n_+ + \alpha_0$ and $\beta = n_- + \beta_0$, where n_+ is the number of green samples and n_- is the number of red samples. The posterior over *r* is:

$$p(r|n_+, n_-) = Beta(r; \alpha, \beta)$$

Investing results in either reciprocation (outcome = 1 with probability *r*, then the investment amount is multiplied by m = 2) or betrayal (outcome = 0 with probability 1 - *r*, then the investment amount is multiplied by m = 0). The agent does not know *r* and therefore has to marginalize over *r*, using the current posterior. This gives the conditional distribution of outcome given α and β:

$$p(\text{outcome} = 1|\alpha, \beta) = \int p(\text{outcome} = 1|r)p(r|\alpha, \beta)dr = \int rp(r|\alpha, \beta)dr = \frac{\alpha}{\alpha+\beta} \quad (1)$$

The expected utility of *not* investing is $U_0 = 1$. The expected utility of investing, U_1, with a free parameter λ for risk attitude becomes:

$$\begin{aligned} U_1(\alpha, \beta) &= \text{E}[\text{outcome}|\alpha, \beta] - \lambda\text{Var}[\text{outcome}|\alpha, \beta] \\ &= \frac{m\alpha}{\alpha + \beta} - \frac{\lambda m^2 \alpha\beta}{(\alpha + \beta)^2} \end{aligned} \quad (2)$$

The agent can decide between sampling (a = 1) or stopping (a = 0) at any time except when t = T+1, then all boxes are opened and only stopping (a = 0) is possible. The value of a state-action pair is given by the Bellman equations (Bellman, 1952). Specifically, the expected value of the state (α,β,) is the higher of the expected utilities of not investing and investing:

$$Q_t(\alpha, \beta; a = 0) = max\{U_0, U_1(\alpha, \beta)\} \quad (3)$$

When t = T+1, the value of the state ($\alpha + \beta$) is $V_t(\alpha, \beta) = Q_{T+1}(\alpha, \beta; a = 0)$. At earlier times, V_t is the larger of the expected utilities:

$$V_t(\alpha, \beta) = max\{Q_t(\alpha, \beta; a = 0), Q_t(\alpha, \beta; a = 1)\} \quad (4)$$

The expected value of a sampling action (a = 1) at time *t* in the state α, β subtracting the subjective cost of a sample *c* is:

$$Q_t(\alpha, \beta;\ a = 1) = \frac{\alpha V_{t+1}(\alpha + 1, \beta) + \beta V_{t+1}(\alpha, \beta + 1)}{\alpha\ +\ \beta} - c \quad (5)$$

By starting with the final state (when *n*, we can obtain the Sample Cost solution for every possible state (dynamic programming). In the Sample Cost model, the decision variable (DV), is the difference between the utilities of sampling and stopping:

$$DV(\alpha, \beta) = Q_t(\alpha, \beta; a = 1) - Q_t(\alpha, \beta; a = 0) \quad (6)$$

The Sample Cost policy would be to sample when the DV is positive; however, we introduce decision noise through a softmax function:

$$p(\text{sample}|\alpha, \beta) = \frac{1}{1 + e^{-\frac{DV(\alpha,\beta)-k}{\tau}}}$$

This model version has six free parameters: α_0, β_0, c, λ, τ and k which were fitted for each subject.

The Threshold model

In the *Threshold Model,* the agent keeps track of the absolute difference between positive and negative information and stops sampling when this difference reaches a bound. However, to be consistent with our other models and with most of the value-based decision literature, we use soft rather than hard bounds. The bound *b* takes three possible values, depending on the sign of $n_+ - n_-$:

$$b = \begin{cases} b_+ & \text{if } n_+ > n_- \\ \frac{b_+ + b_-}{2} & \text{if } n_+ = n_- \\ b_- & \text{if } n_+ < n_- \end{cases} \tag{7}$$

The probability that the agent stops sampling is a logistic function of the difference between this decision variable and a bound *b*:

$$p(\text{sample}|n_+, n_-) = \frac{1}{1 + e^{-\frac{DV(n_+,n_-)-b}{\tau}}} \tag{8}$$

This model version has three free parameters: b_+, b_-, and τ which were fitted for each subject.

The Count model

In the count model, the agent takes a fixed number of samples *k* with some variation. This model represents a simple heuristic where the decision to sample another tile is not determined by the outcomes of the previous samples. We added this model to test if some individuals and especially younger participants might have a strategy of for example always sampling five tiles before making their decision to trust or not trust. The softmax function allows for decision noise:

$$p(\text{sample}|n_+, n_-) = \frac{1}{1 + e^{\frac{(n_+ + n_-)-k}{\tau}}} \tag{9}$$

This model has two free parameters: k and τ which were fitted for every subject.

Within-model comparisons results

For each model, we first fitted the basic version - the version with the fewest free parameters - and then tested whether adding a free parameter significantly improved the model fit (also see (Ma et al., 2018) for more details). The assessment of these additional free parameters was based on the trust game literature. Here, we describe the additionally tested free parameters for each model across all participants. The *Count model* is not included in the within-model comparisons, as it only had one version of the model, which had two free parameters; one for the fixed number of samples and one for variability.

Uncertainty model: prior beliefs improve the model fit. For the same reasons as described earlier, we tested the improvement in model fit when adding a prior belief, also estimated for each subject. In the basic version of our model, we used an uninformative, uniform prior (i.e., $a_0 = 1$ and $b_0 = 1$). In the model version with prior beliefs, we fitted a_0 and b_0 as free parameters for every subject. We found that allowing for a subjective prior improved the model fit (Table S1). The median of individual prior means was $r = 0.47$ (bootstrapped 95% CI [0.45, 0. 50]).

Sample Cost model: prior beliefs and risk attitude both improve the model fit. The repeated trust game literature suggests that subjective prior beliefs (Chang et al., 2010) and betrayal aversion (Aimone & Houser, 2012) both play important roles in determining individual differences in trust. In our paradigm, an individual's prior belief about trustworthiness is a beta distribution with two free parameters (a_0 and b_0). Betrayal attitude is operationalized as the variance of the outcome, multiplied by a free parameter l, which is subtracted from the expected utility of trusting. The median betrayal attitude parameter was estimated at 0.16 (bootstrapped 95% CI [0.10, 0.23]), which shows that participants were overall betrayal-averse.

Threshold model: asymmetric bounds but not collapsing bounds improved the model fit. The literature on Drift Diffusion Models in perception literature suggests that the model fits better with collapsing bounds that reflect an urgency signal (Tajima et al., 2016), or asymmetric bounds (Mulder et al., 2012) as positive sample outcomes might be weighted differently than negative outcomes. Using separate bounds for positive than for negative samples did indeed improve the model fit. Second, we tested the model when the bounds "collapse" to zero over time. This did not improve the model fit from the model with asymmetric bounds.

Table S1.1. Within-model comparison results.

		95% CI	
	Summed ΔBIC	Lower bound	Upper bound
Uncertainty basic vs. priors	2013	925	3316
Sample Cost basic vs. risk attitude	1597	1006	2293
Sample Cost risk attitude vs. risk attitude + priors	791	398	1205
Threshold basic vs. two bounds	44987	38479	51847
Threshold collapsing bound vs two bounds	847	501	1198

95% CI = Bootstrapped 95% confidence interval of the summed difference between model fits. Smaller BIC values indicate better fit. Thus, positive values indicate a better fit for the second model. The models were fitted to the data at the individual level using a log likelihood optimization algorithm as implemented in the fmincon routine in MATLAB (ÓMathworks). The optimization was iterated 100 times with varying initiations to avoid local minima. Because of the summation of the difference, large positive or negative numbers therefore reflect that one model wins consistently, i.e. for most subjects.

Between- model comparison results

We then compared the best fitting version of each model with the best fitting model of the other models. Table S2 shows the results which indicate that the Uncertainty model fitted best.

Table S1.2. Between model comparisons.

Pairwise comparison between models	**Summed ΔBIC and 95% CI**	**Winning model**	**Correlation between age and ΔBIC**
Uncertainty - Sample Cost	-1685 [-3086, -527]	**Uncertainty**	r_s = -0.059, p = .464
Uncertainty - Threshold	-1741 [-3072, -636]	**Uncertainty**	r_s = 0.101, p = .221
Uncertainty - Count	-51940 [-55095, -48774]	**Uncertainty**	r_s = -0.349, p < .001
Sample Cost - Threshold	-56 [-627, 504]	**None**	r_s = 0.031, p = .711
Sample Cost - Count	-50243[-52923, -47489]	**Sample Cost**	r_s = -0.385, p < .001
Threshold - Count	-50151[-52836, -47349]	**Threshold**	r_s = -0.364, p < .001

Lower BIC values indicate a better fit, thus showing that the Uncertainty model fits significantly better than all other models. BIC scores were computed for each participant and each model. The BIC scores of a model pair (left column) was then subtracted from each other, thereby obtaining one difference score per participant for each model pair. The middle column shows the sum of the difference across participants and the 95% confidence interval of the BIC difference, computed using bootstrapping with 10^5 iterations. The last column shows the Spearman-rank correlation between age and each model pair's BIC difference.

Descriptive statistics number of samples

The descriptive statistics were obtained through generalized linear mixed models in R (package LME4). We assessed the fit of polynomial models (linear, quadratic) using the anova() function in R. For the number of samples, the linear age model fitted better than the polynomial (linear and quadratic) models.

For the analyses of the number of samples, we first calculated the outcome uncertainty, which is the variance in the Bernoulli distribution:

$$\text{Outcome uncertainty} = r(1- r)$$

Where r is the probability of reciprocation.

For transparency we report the full mixed effects model in R code here:
SamplingModel <- lmer(number of samples ~ scale(outcome uncertainty) * scale(age) + (1| subject), data = df)

Table S2.1. Results number of samples mixed model

Predictors	Sample decisions		
	β	*95% CI*	*p*
Intercept	16.21	15.37 – 17.05	**<.001**
Outcome uncertainty	2.10	2.00 – 2.20	**<.001**
Age	-0.47	-1.31 – 0.37	.276
Outcome uncertainty x Age	0.42	0.32 – 0.52	**<.001**
Random Effects			
σ^2	24.46		
$\tau_{00\ \text{subject}}$	28.44		
ICC	0.54		
N_{subject}	157		
Observations	9420		
Marginal R^2 / Conditional R^2	0.083 / 0.579		

Post hoc test for the number of samples

To further examine the interaction effect, we created age bins consistent with Figure 2C and compared the slopes for outcome uncertainty between the age groups using the emtrends() function. This showed that only the early adolescents differed significantly from all other age groups (Table S2.2). We used the following code:
emtrends(SamplingModel, pairwise ~ ageGroup, var="outcome uncertainty")

We also created bins for the probability of reciprocation consistent with Figure 2C and used the emtrends() function to compare the slopes of the age effect between the different reciprocation probabilities. The effect of age on the number of samples was strongest in the highest and lowest reciprocation probabilities (Table S2.2). We used the following code: emtrends(ReciprocationModel, pairwise ~ reciprocation probability bins, var="age")

Table S2.2. Results post-hoc pairwise comparison per age group

Contrast age groups	**estimate**	***t* ratio**	***p*-value**
10-12 vs 13-15	-9.217	-5.722	<.0001*
10-12 vs 16-18	-12.081	-7.441	<.0001*
10-12 vs 19-20	-8.619	-5.351	<.0001*
10-12 vs 21-24	-14.565	-8.971	<.0001*
13-15 vs 16-18	-2.863	-1.778	.387
13-15 vs 19-20	0.598	0.375	.996
13-15 vs 21-24	-5.348	-3.320	.008
16-18 vs 19-20	3.462	2.149	.120
16-18 vs 21-24	-2.484	-1.530	.543
19-20 vs 21-24	-5.946	-3.691	.002*
Contrast reciprocation probability	**estimate**	***t* ratio**	***p*-value**
0-0.2	-0.087	-2.180	.247
0-0.4	-0.194	-4.833	<.0001*
0-0.6	-0.189	-4.712	<.0001*
0-0.8	-0.021	-0.521	.995
0-1.0	0.104	2.595	.099
0.2-0.4	-0.106	-2.653	.085
0.2-0.6	-0.102	-2.532	.115
0.2-0.8	0.067	1.659	.559
0.2-1.0	0.192	4.775	<.0001*
0.4-0.6	0.005	0.121	1.000
0.4-0.8	0.173	4.312	<.001*
0.4-1.0	0.298	7.428	<.0001*
0.6-0.8	0.168	4.191	<.001*
0.6-1.0	0.293	7.307	<.0001*
0.8-1.0	0.125	3.116	.023

Note: **p*-values are significant at the Bonferroni-holm corrected level.

Descriptive statistics invest decisions

For the invest decisions, the model with the linear effect of age also fitted better than the model with the polynomial effects of age (linear and quadratic). The mixed effects model was specified as follows:

InvestModel <- glmer(Invest decision ~ scale(reciprocation probability) * scale(age) + (1| subject), data = investdata, family = binomial, control = glmerControl(optCtrl = list(max-fun = 1e+9), optimizer = c("bobyqa")))

Table S2.3. Results invest decisions mixed model

Predictors	*Odds Ratios*	*95% CI*	β	*p*
Intercept	0.62	0.53 – 0.72	-0.478	**<.001**
Reciprocation probability	30.38	26.15 – 35.28	3.414	**<.001**
Age	0.99	0.85 – 1.15	-0.011	.888
Reciprocation probability x age	2.36	2.07 – 2.70	0.860	**<.001**
Random Effects				
σ^2	3.29			
$\tau_{00\ subject}$	0.73			
$ICC_{subject}$	0.18			
$N_{subject}$	157			
Observations	9420			
Marginal R^2 / Conditional R^2	0.755 / 0.800			

Post hoc test for invest decisions

We were interested in whether the effect of age was present in all reciprocation probabilities. We therefore conducted post hoc tests per probability of reciprocation using the lmer() function in R for each probability of reciprocation separately:

posthoc_model <- lmer(Invest decision ~ scale(age) + (1| subject), data = df_reciprocationBin)

This showed that the effect of age was only significant when the probability of reciprocation was high (0.8 and 1.0) or lowest (0.0, see Table S2.3).

Table S2.4 post hoc test for the effect of age on invest decisions per reciprocation probability

Probability of reciprocation	estimate	*t* value	*p*-value
0.0	-0.020	-3.333	.001*
0.2	-0.018	-2.312	.022
0.4	-0.010	-0.691	.491
0.6	0.020	0.999	.319
0.8	0.044	4.733	<.0001*
1.0	0.040	5.108	<.0001*

Note: **p*-values are significant at the Bonferroni-holm corrected level.

Expected reward increased with age

We examined if the expected values based on the trust decisions varied with age. We first normalized the outcomes on the endowment of 6 tokens. Thus, the expected value for not investing is 1. The expected value for investing is computed as the multiplier of 2 times the reciprocation probability. Since the reciprocation probabilities were 0.0, 0.2, 0.4, 0.6, 0.8, and 1.0, the possible average expected values ranged from $\frac{0 + 0.4 + 0.8 + 1 + 1 + 1}{6} = 0.67$ to $\frac{1 + 1 + 1 + 1.2 + 1.6 + 2}{6} = 1.3$. All subjects (with exception of one), had an average expected reward higher than 1 (see Figure S1). This confirms that all subjects would - on average - have gained money on top of their original endowment by trusting when trusting was beneficial. However, younger adolescents earned less on this task than older adolescents, consistent with their deviations in low (0.0) and high (0.8, 1.0) investment probabilities. This was shown by a significant correlation between age and the average expected reward in the task ($r_s = 0.387$, $p < .001$).

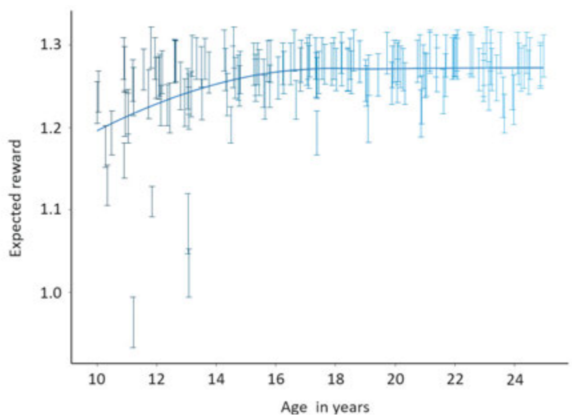


Figure S1. Expected reward per subject as function of age. The expected reward increases with age. Error bars indicate the s.e.m. The line and shaded region indicates the mean and s.e.m across subjects. Color indicates age in months.

Age-related changes in Uncertainty model parameter estimates

Linear regressions were used to examine the relationship between age and the Uncertainty model parameter estimates using the lm() function in R. We first tested whether adding age as a quadratic term with the poly() function improved the model fits when compared to a linear term only using the anova() function in R (Phillips, 2017). For the prior uncertainty the quadratic term did improve the model fit ($F(1,154) = 6.835$, $p = .010$). For all other parameter estimates the quadratic effect of age did not improve the model fit (prior mean $F(1,154) = 3.861$, $p = .051$; uncertainty tolerance $F(1,154) = 1.940$, $p = .166$; decision noise $F(1,154) = 2.255$, $p = .119$). We applied a Bonferroni-holm correction for multiple testing, which includes the model improvement test for each of the four parameters, a linear age effect test for three of these parameters, and two test (linear and quadratic age effects) for one parameter, corresponding to a total of 9 tests.

Model recovery

We performed model recovery and verified that the models were distinguishable. To this end, we simulated data with each model and subsequently fitted the simulated data to each model. If the model is recoverable, then the best fitting model should be the model that generated the data. We show that this was indeed the case as the model fit was always best for the model that generated the data (Table S3.1).

Parameter recovery

To check if the parameters were recoverable, we simulated data with each model using varying parameter values as inputs. We randomly selected the estimates of 20 subjects to simulate data with an equal number of trials as in the actual task. We then fitted that simulated data to the model to check if the parameters values that generated the data were correctly estimated. We subtracted the estimated parameters of the simulation from the actual input parameters and calculated the bootstrapped 95% confidence interval and found no significant difference between the input parameters and the estimated parameter values. This returned: Uncertainty tolerance median difference = -0.0001, 95% CI [-0.000, 0.000]; a_0 median difference = -0.386, 95% CI [-0.590, 0.000]; b_0 median difference = -0.250, 95% CI [-0.580, 0.000]). This suggests that the parameters were indeed recoverable.

Table S3.1. Model recovery results

		95% CI	
	Summed ΔBIC	Lower bound	Upper bound
Data generated by the Uncertainty model			
Uncertainty vs. Sample Cost	-849	-1057	-654
Uncertainty vs. Threshold	-568	-861	-293
Uncertainty vs Count	-7014	-8129	-5859
Data generated by the Sample Cost model			
Sample Cost vs. Uncertainty	-795	-313	-541
Sample Cost vs. Threshold	-537	-908	-249
Sample Cost vs Count	-7350	-8675	-5978
Data generated by the Threshold model			
Threshold vs. Sample Cost	-827	-964	-689
Threshold vs. Uncertainty	-654	-894	-448
Threshold vs Count	-6102	-6923	-5179
Data generated by the Count model			
Count vs. Sample Cost	-2193600	-2195896	-2191370
Count vs. Uncertainty	-2563	-2917	-2224
Count vs. Threshold	-2190400	-2192665	-2188118

95% CI = Bootstrapped 95% confidence interval of the summed difference between model fits. Negative values indicate a better fit of the model that generated the data. The data were generated using the participants' parameter estimates and shows that all models were recoverable.

5

Chapter 5

Increased ventromedial prefrontal cortex activity in adolescence benefits prosocial reinforcement learning

This chapter is published as:

Westhoff, B., Blankenstein, N. E., Schreuders, E., Crone, E. A., & van Duijvenvoorde, A. C. K (2021). Increased ventromedial prefrontal cortex activity in adolescence benefits prosocial reinforcement learning. *Developmental Cognitive Neuroscience*, 52, 101018. https://doi.org/10.1016/j.dcn.2021.101018

Abstract

Learning which of our behaviors benefit others contributes to forming social relationships. An important period for the development of (pro)social behavior is adolescence, which is characterized by transitions in social connections. It is, however, unknown how learning to benefit others develops across adolescence and what the underlying cognitive and neural mechanisms are. In this functional neuroimaging study, we assessed learning for self and others (i.e., prosocial learning) and the concurring neural tracking of prediction errors across adolescence (ages 9-21, N=74). Participants performed a two-choice probabilistic reinforcement learning task in which outcomes resulted in monetary consequences for themselves, an unknown other, or no one. Participants from all ages were able to learn for themselves and others, but learning for others showed a more protracted developmental trajectory. Prediction errors for self were observed in the ventral striatum and showed no age-related differences. However, prediction error coding for others showed an age-related increase in the ventromedial prefrontal cortex. These results reveal insights into the computational mechanisms of learning for others across adolescence, and highlight that learning for self and others show different age-related patterns.

Introduction

Adolescence is a developmental phase that is characterized by transitions in social connections, and moreover, a phase during which social cognitive skills are acquired and/or improved (Blakemore & Mills, 2014; Casey et al., 2008; Crone & Dahl, 2012; Sawyer et al., 2018). As social acceptance and approval from peers often result from displaying prosocial behaviors, for adolescents establishing their social network it is key that they learn to help or benefit others (Steinberg & Morris, 2001). That is, to be able to behave in a prosocial manner, individuals need to learn which actions would result in positive outcomes for others. This type of learning is also referred to as prosocial learning (Lockwood et al., 2016; Sul et al., 2015). Generally speaking, learning from actions and outcomes is an important part of cognitive development and continues to improve in adolescence (Bolenz et al., 2017; Nussenbaum & Hartley, 2019; Peters, Braams, et al., 2014; Peters et al., 2016). For adolescents, an especially salient environment that requires learning about the consequences of their actions is the interpersonal context (Blakemore & Mills, 2014; Nelson et al., 2005; Sawyer et al., 2018). Therefore, it is expected that especially prosocial learning shows improvements in adolescence. The goal of the current study was to unravel age-related differences in learning to benefit others using a prosocial learning context across adolescence.

The vast majority of recent neuroscientific studies investigating learning make use of formal reinforcement learning (RL) models. These models calculate individuals' prediction errors (PEs) – the difference between expected and actual outcomes - over the course of learning. These PEs drive learning via a learning rate, which quantifies to what extent these PEs affect subsequent actions. Consequently, RL models and the resulting PEs enable studies to examine the neural tracking of value-guided decision-making. Neuroscientific studies demonstrated that PE coding in a probabilistic reinforcement task context is associated with activation in the ventral striatum, as well as the medial prefrontal cortex (mPFC) (see for reviews e.g., (Cheong et al., 2017; Joiner et al., 2017; Lockwood & Klein-Flügge, 2020; Olsson et al., 2020; Ruff & Fehr, 2014). Developmental studies using RL models found that adolescents show similar neural tracking of PEs as adults when learning stimulus-outcome associations. However, the developmental patterns are inconsistent: some studies have reported elevated or lowered PE activity in the ventral striatum and connected structures in mid-adolescents relative to children and adults (Cohen et al., 2010; Davidow et al., 2016; Hauser et al., 2015; Jones et al., 2014), but this is not replicated in all studies (Christakou et al., 2013; van den Bos, Cohen, et al., 2012). Furthermore, age-related differences have been found in functional connectivity between the ventral striatum and mPFC, here referred to as ventromedial PFC (vmPFC), in relation to learning (van den Bos, Cohen, et al., 2012), suggesting that age-related improvements in learning are associated with stronger neural coupling between subcortical and cortical brain regions (van Duijvenvoorde et al., 2016, 2019). Taken together, previous studies point to the ventral striatum and medial prefrontal cortex as important brain areas for learning in non-social environments.

Previous studies investigating the neurocomputational mechanisms of prosocial learning have investigated whether the same neural signaling occurs for PEs for others as for self. Recently, in adults, it was found that PE tracking for both learning for others as for self occurred in the ventral striatum (Lockwood et al., 2016). However, the subgenual anterior cingulate cortex (sgACC) specifically coded PE tracking for learning for others, and these prosocial learning signals were predicted by cognitive empathy. That is, more empathic people showed more activity in the sgACC when learning to benefit others. Cognitive empathy – the ability to understand the emotional states of others (Netten et al., 2015; Pouw et al., 2013) - shows pronounced changes in adolescent development and relates positively to prosocial behaviors such as trust and reciprocity (Dumontheil et al., 2010; Eisenberg et al., 1995; van de Groep et al., 2018). Therefore, we aimed to extend prior work by Lockwood and colleagues (2016) by investigating the neural tracking of PEs for others, and its relation with individual differences in cognitive empathy, in an adolescents sample with participants aged between 9 and 21 years.

In the current study, we adopted a prosocial learning task (Lockwood et al., 2016) in which participants could learn to obtain rewards for themselves, others, or no one. We administered this task to 74 adolescents between ages 9-21 years to examine age-related differences in learning for self and others, combined with functional neuroimaging (fMRI) for neural tracking of PEs. We use the term adolescence for this broad age range, based on definitions that mark adolescence from the onset of puberty to the age when one reaches independence from parents (i.e., approximately 9-24 years; e.g., Sawyer et al., 2018). Based on prior studies, we performed regions-of-interest analyses for the ventral striatum, sgACC, and vmPFC. We expected that adolescents, similar to adults, would show PE related neural activity when learning both for self and others in the ventral striatum (Lockwood et al., 2016), and in the sgACC and possibly vmPFC when learning for others more than when learning for self (Christopoulos & King-Casas, 2015; Lockwood et al., 2016). For learning for self, research has remained inconclusive whether this activity peaks in mid-adolescence (Cohen et al., 2010; Davidow et al., 2016) or shows no age-related differences (van den Bos, Cohen, et al., 2012). Therefore we explored linear as well as non-linear (quadratic) age effects. We predicted that sgACC and vmPFC activity for prosocial learning would increase with age, based on prior studies showing age-related improvements in social-cognitive perspective-taking (Dumontheil et al., 2010). Finally, consistent with (Lockwood et al., 2016), we expected that individual differences in cognitive empathy would relate to neural tracking of PEs for others.

Methods and Materials

Participants

A total of 76 participants between ages 9 and 21 took part in this study. Participants were recruited through schools and local advertisements, as well as from participation in a previous study. Two participants were excluded from analyses because they were either diagnosed with a psychiatric disorder at the time of testing (n = 1) or because the session was stopped early due to discomfort in the scanner (n = 1). We did not exclude participants based on task performance; there were no significant outliers in task performance (i.e., >3 SD) in any of the conditions. Four participants missed one run of the task, due to technical issues (n = 2), or discomfort in the scanner (n = 2). These four participants were maintained with the available data in all analyses. The final sample included 74 healthy participants (39 female, M_{age} = 15.64, SD_{age} = 4.18, range = 9.03 – 21.77 years, see Figure S1 for an overview of the number of participants across ages). The IQ scores, estimated with the Similarities and Block Design subtests of the WISC-III and WAIS-III, fell within the normal range (M_{IQ} = 110.24, SD_{IQ} = 10.37, range = 87.50 - 135.00), and did not correlate with age ($r(72) = -0.11$, p = .353).

The local institutional review board approved this study (reference: NL56438.058.16). Adult participants and parents of minors provided written informed consent, and minors provided written assent. All anatomical scans were cleared by a radiologist and no abnormalities were reported. Participants were screened for MRI contraindications and psychiatric or neurological disorders, and had normal or corrected-to-normal vision.

Prosocial learning task

Participants played a two-choice probabilistic reinforcement learning task (prosocial learning task) in the MRI scanner (see Figure 1A). Participants were instructed to make a series of decisions between two pictures. One picture was associated with a high probability of winning 1 point, the other picture with a high probability of losing 1 point. The exact probabilities were 75% and 25% but were unknown to the participant. After the decision, participants were presented with the outcome to enable them to learn the reward contingencies.

The participants played the task in three different conditions: for themselves (Self), for an unknown other participant (Other), or for No One. The latter condition was added as a control condition based on Lockwood et al. (2016). Participants did not meet the other person, but were told that the other person was a peer also participating in the experiment who i) would not play the same game for them, ii) did not know who played for them (see Participant instructions in the Supplementary materials). Each block started with an instruction screen that indicated who would receive the outcomes (Self, Other, or No One) for 2000 ms. This was followed by the presentation of two stimuli for 2500 ms during which participants were required to select one of these. The stimuli were common objects, such as chairs, apples, and shoes (see also Van Den Bos et al., 2009). If no response was given within the time frame, the text "Too late" appeared in the middle of the screen, and these trials were excluded from analyses.

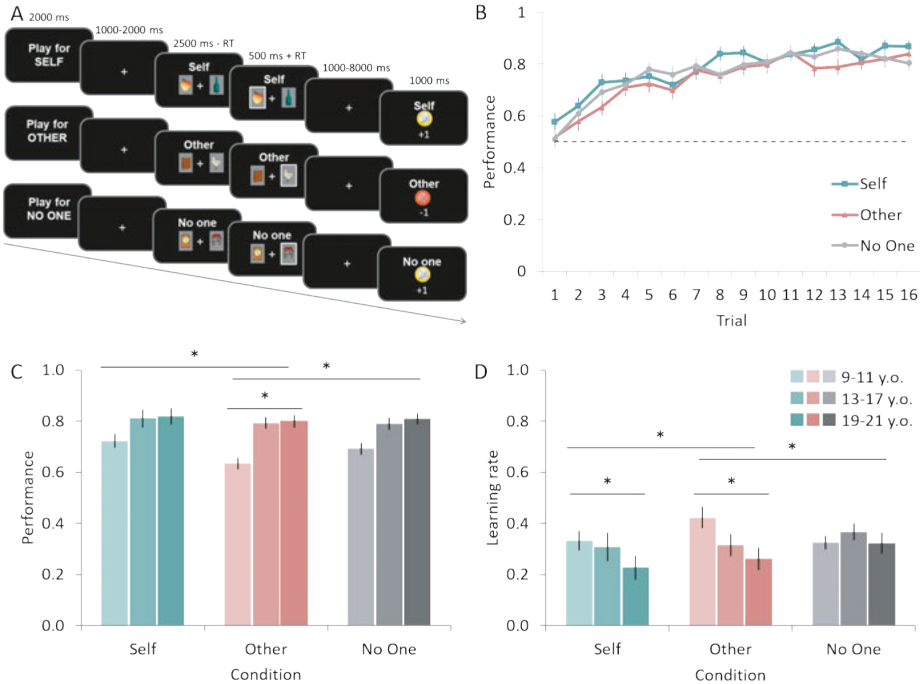


Figure 1. Prosocial learning task and behavioral data. **(A)** Participants played a two-choice probabilistic reinforcement learning task in which outcomes resulted in monetary consequences for themselves (Self condition), for an unknown other participant in the experiment who could not reciprocate (Other condition), or for No One. **(B)** Group-level performance across trials (learning curves) per condition, averaged across blocks. Performance represents the fraction of selecting the stimulus with a high reward contingency. The dashed line indicates performance at chance level (0.5). **(C)** Performance per condition per age cohort, averaged across the entire task. In all conditions, performance improved across trials, but an age-related increase was only observed when learning for others. Note that age is used as a continuous variable in all analyses but is visualized as age cohorts for illustrative purposes. The age-related increase was greater for the Other than for the Self and No One condition. **(D)** Learning rates per condition per age cohort. Age-related decreases in learning rates are only observed in the Self and Other condition. The age-related decrease in learning rate was greater in the Other compared to the Self and No One condition. Asterisks indicate significant effects. Error bars represent standard error of the mean (s.e.m.).

A selection frame around the chosen picture confirmed the response and remained visible for the duration of the interval and an additional 500 ms. A fixation screen (duration randomly jittered between 1000-2000 ms) preceded the outcome of their choice (+1 point or -1 point; 1000 ms). A randomly jittered fixation screen (1000-8000 ms) was shown after the outcome before the two pictures were presented again. The screen position of the stimulus (left or right) was counterbalanced across trials. Participants were instructed that the position of the stimulus did not matter, to encourage them to learn the reward contingencies regardless of stimulus position.

There were 144 trials in total, 48 for Self, 48 for Other, and 48 for No One, presented in three blocks of 16 trials. Each block began with a new pair of pictures. Participants completed three separate fMRI runs with a short break in between, each with one block of 16 trials per condition. The order of the conditions was counterbalanced across runs and between participants.

Participants were instructed that the total number of points in the Self condition was converted to money (each point valued €0.25), which they would get paid out on top of their flat participation rate (€20 for 9-11 y.o., €25 for 13-17 y.o., and €30 for 19-21 y.o.). The minimum of this extra amount of money was €1 to avoid null scores, and the maximum was €12. Additionally, participants were instructed that their choices in the Other condition were paid out to a participant entering the experiment after them. Consequently, participants received an additional fee from a participant before them in the experiment (minimum €1 and maximum €12), but only at the end of the experiment. Finally, it was instructed that choices in the No One condition had no financial consequences.

Cognitive empathy

To assess cognitive empathy, participants completed the Interpersonal Reactivity Index (IRI; Davis, (1983). This widely used self-report questionnaire consists of 4 subscales (Perspective-Taking and Fantasy as cognitive empathy subscales; and Personal Distress and Empathic Concern as affective empathy subscales) with 6 items each. To create a measure of cognitive empathy, two subscales were combined (Pulos et al., 2004): the Perspective-Taking subscale (e.g., “I sometimes try to understand my friends better by imagining how things look from their perspective”, Cronbach’s alpha = 0.710) and the Fantasy subscale (e.g., “I really get involved with the feelings of the characters in a novel”, Cronbach’s alpha = 0.786). All items can be answered on a five-point Likert scale ranging from (0) not true at all to (4) completely true, and higher scores indicate higher levels of empathy. Cognitive empathy scores increased across age (r = .309, p = .008, see Figure S8). One person did not fill in this questionnaire. This person was excluded from further analyses concerning measures of (cognitive) empathy. We used a Dutch adolescent version for all ages in our study, with items adapted for the youngest ages in the study (Hawk et al., 2013).

Procedure

Participants were accustomed to the MRI environment using a mock scanner, and received instructions on the prosocial learning task in a quiet laboratory room. Instructions for the task were displayed on a screen and read out loud by an experimenter. Participants completed 8 practice trials in each condition. In the scanner, participants responded with their right hand using a button box. Head movements were restricted with foam padding. The fMRI scan was accompanied by a high-definition structural scan. Questionnaires were filled out at their home prior to the scanning session, via Qualtrics (www.qualtrics.com).

Computational modeling of behavioral data

Model fitting

We used MATLAB 2015b (The MathWorks Inc) for all model fitting and comparison. We modeled learning behavior in the Self, Other, and No One conditions separately, using a standard Rescorla-Wagner reinforcement learning (RL) model (similar to Lockwood et al., 2016) to obtain PEs and learning rates, which were subsequently used in behavioral and fMRI analyses. Simple RL models state that the expected value of a future action (Q_{t+1}(i)) should be a function of current expectations (Q_t(i)) and the difference between the actual reward that has been experienced on this trial (R_t). The learning rate α, bounded between 0 and 1, determines how much the value of the chosen stimulus is updated based on the new outcome. In particular, the learning rate parameter speeds up or slows down the acquisition and updating of associations. Optimal learning rates differ between contexts and reinforcement structures (Nussenbaum & Hartley, 2019).

$$Q_{t+1}(i) = Q_t(i) + \alpha * \underbrace{[R_t - Q_t(i)]}_{\substack{\text{prediction} \\ \text{error}}}$$

To select an action based on the computed values, we used a standard softmax choice function. For a given set of parameters, this equation allows us to compute the probability of the next choice being "i":

$$P_t(i) = \frac{e(\beta * Q_{i,t})}{\sum_j e(\beta * Q_{j,t})}$$

Beta (β) determines *how strongly* action probabilities are guided by their expected values (Q). Here, with larger β, actions are more deterministic and driven by expected values, resulting in selecting the option with the highest value. With lower β, actions are more random or exploratory. This parameter thus affects errors, where a decrease will lead to more random (i.e., less driven by expected values) choices. β did not differ between conditions, although with age, people were more strongly driven by expected values (see Figure S2 for the β across age cohorts for each condition).

We used the maximum a posteriori (MAP) approach (Daw, 2011) for fitting the RL model to participants' choices per condition. To facilitate stable estimation across subjects, we used weakly informative priors to regularize the estimated priors toward realistic ones. These weakly informative priors and estimation procedures were based on previous research (den Ouden et al., 2013), and included a Beta (1.2, 1.2) distribution for the estimated α (learning rate) parameter ($0 < \alpha < 1$) and a Gaussian distribution (0, 10) for the estimated β parameter ($-\infty \leq \beta \leq \infty$). Mean and confidence intervals for each of the fitted parameters across all subjects are displayed in Supplementary Table S1.

Model comparison

Based on previous developmental findings (e.g., van den Bos et al., 2012) we compared an alternative model with two learning parameters (i.e., separate learning rates for gains and losses) in order to benchmark the performance of the one-learning parameter model (i.e., one learning rate). Model comparisons revealed that the one-learning parameter model had a superior fit to the behavioral data for each condition, according to the Bayesian Information Criterion (BIC) (see Figure S3). This was the case in each condition for the majority of the participants (81.1% Self, 74.3% Other, 76.7% No One), in all age cohorts, see Figure S3. In none of the conditions, the BIC difference scores (Figure S3) were correlated with age (r_s, all p values > .14).

Simulations and parameter recovery

To assess whether computational model parameters could be successfully recovered, we simulated choice behavior for the range of learning rates and beta's that we encountered in our dataset. That is, we simulated a new participant dataset based on the α and β values from our participants as input parameters. This resulted in a simulated dataset with 74 participants. Parameter recovery, as indicated with correlations between simulated and recovered learning rates and beta values per conditions, is presented in Figure S4.

Behavioral analyses

To assess learning for Self, Other, and No One, and their developmental patterns in the prosocial learning task, we fitted logistic generalized linear mixed models (GLMMs) to decisions (correct coded as 1, incorrect as 0) for each condition separately. These analyses were conducted in R version 4.0.1 (R Core Team, 2020), using the lme4 package (Bates et al., 2014). Our GLMMs included fixed effects of Age in years (linear and quadratic), Condition, Trial, and all interactions. Since no significant main or interaction effects of age-quadratic were observed in the choice data, this term was dropped in the final presented behavioral models for model parsimony. In all models, participant ID entered the regression as a random effect to handle the repeated nature of the data. Where applicable, Trial was additionally included as a random slope per subject. We performed post hoc tests using the *emmeans* package (Lenth et al., 2021), as well as tests per condition to delineate Age x Trial x Condition effects.

Next we examined the estimated learning rates per condition. These parameters indicate how people updated the value of stimuli based on outcomes for Self, Others, and No One. Since learning rates were not normally distributed, we used a robust linear mixed effects model (RLMM, rlmer function, robustlmm package (Koller, 2016) in R (see also Cutler et al., 2021), with Condition and Age linear as fixed main effects and interaction effects. We performed post-hoc tests per condition and pair-wise contrasts per Condition. In all GLMM and RLMM models, continuous independent variables were mean-centered and scaled, and categorical predictor variables were specified by a sum-to-zero contrast (e.g., sex: -1 = boy, 1 = girl). P-values for the GLMM were generated by using the Anova log-likelihood ratio tables from the afex package (Singmann et al., 2019). For the RLMM models, the Satterthwaite-approximated degrees of freedom generated by the lme4 model in combination with the output of the RLMM, was used to generate P-values.

Finally, we assessed whether cognitive empathy related to learning performance, learning rate, and PE activation when learning for others. We ran (partial) spearman correlational analyses with learning for self and cognitive empathy as predictors using the package 'ppcor' (Kim, 2015).

fMRI acquisition

For acquiring (functional) MRI data, we used a 3T Philips scanner (Philips Achieva TX) with a standard eight-channel whole-head coil. The learning task was projected on a screen that was viewed through a mirror on the head coil. Functional scans were acquired during three runs of 200 dynamics each, using T2* echo-planar imaging (EPI). The volumes covered the entire brain (repetition time (TR) = 2.2 s; echo time (TE) = 30 ms; sequential acquisition, 38 slices; voxel size 2.75 x 2.75 x 2.75 mm; field of view (FOV) = 220 (ap) x 220 (rl) x 114.68 (fh) mm). The first two volumes were discarded to allow for equilibration of T1 saturation effects. After the learning task, a high-resolution 3D T1 scan for anatomical reference was obtained (TR = 9.76 msec, TE = 4.95 msec, 140 slices, voxel size = 0.875 x 0.875 x 0.875 mm, FOV = 224 (ap) x 177 (rl) x 168 (fh) mm).

Preprocessing

Data were analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London). Images were corrected for slice timing acquisition and rigid body motion. We spatially normalized functional volumes to T1 templates. Occasional framewise displacement >3mm occurred for 3 participants in 1-2 volumes. For those participants with frame-frame head motion >3mm, an extra regressor was included corresponding to each volume (*n* = 3, for maximum 2 volumes). All other participants did not exceed translational head movement more than 3mm in any of the scans (*Mean* = 0.65mm, *SD* = 0.059mm). The normalization algorithm used a 12 parameter affine transform with a nonlinear transformation involving cosine basis function, and resampled the volumes to 3 mm^3 voxels. Templates were based on MNI305 stereotaxic space. The functional volumes were spatially smoothed using a 6 mm full width at half maximum (FWHM) isotropic Gaussian kernel.

General linear model

We used the general linear model (GLM) in SPM8 to perform statistical analyses on individual subjects' fMRI data. The fMRI time series were modeled as a series of two events: the decision phase (Expected Value, EV) and the outcome phase (PE), convolved with a canonical hemodynamic response function (HRF). The onset of the choice (EV), and the onset of the outcome (PE) were both modeled with zero duration. Each of these regressors was associated with a parametric modulator taken from the computational model. At the time a stimulus was selected (decision phase) this was the chosen expected value, and at the time of the outcome, the PE. The PEs were estimated using each subject's own alpha and beta from each condition. Trials on which participants did not respond were modeled separately as a regressor of no interest. Six motion parameters, and -if applicable- motion censoring regressors were included as nuisance regressors. We used the MarsBaR toolbox (Brett, Anton, Valabregue, & Poline, 2002; http://marsbar.sourceforge.net) to visualize the patterns of activation, in clusters identified in the whole-brain results. Coordinates of local maxima are reported in MNI space. Our main hypotheses centered on PE coding. For completeness, effects of EV at choice onset are included in Supplementary Table S3. In addition, uncorrected T-maps of EV and PE effects are uploaded on Neurovault (https://neurovault.org/collections/EOTSVZYT/). For condition effects, we examined contrasts of Self versus Other in concordance with Lockwood et al. (2016). Contrasts were obtained from a flexible factorial design with three levels (Self PE, Other PE, No One PE). Effects and conclusion remained the same when testing Self PE > Other PE + No One PE, and Other PE > Self PE + No One PE. In Supplementary Table S4 we include all contrasts between conditions within our ROIs. Whole-brain effects for main effects and between conditions are included in Supplementary Tables S2 and S5, respectively. Age effects (linear and quadratic) were tested in follow-up regressions.

ROI selection and fMRI analyses

The a priori regions of interest (ROI) in which we test our main hypotheses were defined anatomically and based on previous research on (prosocial) learning and feedback processing (Lockwood et al., 2016; van den Bos, Cohen, et al., 2012; van Duijvenvoorde et al., 2014). In concordance with previous studies, masks were taken from an appropriate atlas. That is, the bilateral ventral striatum and vmPFC were determined by an anatomical mask from the Harvard-Oxford Atlas (van Duijvenvoorde et al., 2014; van den Bos et al., 2012; Braams et al., 2015; Peters & Crone, 2017), and the sgACC was defined as Brodmann areas (BA) 25 and s24 (Lockwood et al., 2016). The sgACC region and the ventral striatum are anatomically adjacent and partly overlapping (see Figure S5), but significant peak activations in either ROI were not observed in these overlapping voxels. Coordinates for local maxima are reported in MNI space. Effects in our ROIs are reported at $p < .05$ FWE-small volume corrected (SVC). Predictions were tested while correcting for multiple comparisons (3 ROIs) by limiting the false discovery rate (FDR; Benjamini & Hochberg, 1995); all reported tests survived this correction. Explorative whole-brain analyses are reported in Supplementary Tables S2 and S5, and Figure S6).

Results

Developmental differences in learning to obtain rewards for Self, Others, or No One

Results showed that, at the group level, participants were able to learn for Self, Other, and No One, as they performed above chance level in all conditions (0.5; *t* values > 13.0, all *p*s < .001, $df = 73$; Figure 1B). Using a generalized linear mixed model (GLMM) on participants' choice behavior over trials, we assessed age-related differences in performance when learning for Self, Other, and No One. Performance in the learning task improved linearly with age (main effect of Age linear, $p = .001$). Moreover, we observed that age-related differences in learning performance differed per condition (Age x Condition interaction, $p = .005$). Post-hoc analyses revealed that the age-related improvement in performance was larger when learning for Other than when learning for Self ($p = .009$) and when learning for No One ($p = .02$). The age-related improvements were similar for learning for Self and No One ($p = .92$). Similarly, we also observed age-related differences in learning curves across trials, which differed per condition (Age x Condition x Trial interaction, $p = .007$). Specifically, younger children learned more slowly (i.e., flatter learning curves) across trials when learning for others, but this age effect on trial was not observed for the Self and No One condition (Age linear x Trial, for Other condition, $p < .001$; Self and No One conditions: *p*s > 0.2; see Figure 1C and Figure S7). Together, these findings suggest that across adolescence prosocial learning shows a more protracted improvement than when learning for Self or No One.

Next, we examined participants' learning rates to assess how they updated the value of stimuli on the basis of outcomes for Self, Others, and No One. That is, higher learning rates indicate that people adjusted behavior quickly towards recent feedback, whereas lower learning rates indicate a slower pace in updating in which outcomes across multiple trials are integrated. Using a robust linear mixed effects model, we assessed effects of Condition and Age (linear) in learning rates (Figure 1D). We observed that learning rates for Self were lower than learning rates for Other ([Self vs Other], $b = 0.02$, $p < .001$) and for No One ([Self vs No One], $b = -0.03$, $p < .001$). Learning rates for Other and for No One did not differ ([Other vs No One], $p = .911$). Moreover, we observed that learning rates decreased linearly with age (main effect of Age linear, $b = -0.04$, $p = .023$), an effect that also differed across conditions. Specifically, learning rates decreased across age in the Other and Self condition, but more strongly across age for Other than for Self ([Other-Self]*Age, $b = -0.02$, $p < .001$) and for Other than for No one ([Other-No One]*Age, $b = 0.004$, $p = .004$). Learning rates also decreased more strongly across age for Self than for No One ([Self-No One *Age, $b = .019$, $p < .001$). Learning rates did not differ across age in the No One condition ($p = .08$). Together, these findings show that for both learning for Self and Others, younger participants responded more to recent feedback, whereas older participants integrated feedback more over trials. Moreover, this age-related change was most pronounced in the Other compared to the Self and No One condition.

5

Identifying common and distinct coding of prediction errors for Self and Others

To formally investigate the brain regions that were responding to PEs for Self, Others, and No One, we conducted a conjunction analysis to explore whether there were regions that commonly code PEs across all conditions. Common activation for PEs regardless of the beneficiary was observed in the vmPFC (MNI coordinates [$x = -9$, $y = 44$, $z = -11$], $Z = 5.33$, $k = 136$, $p < .001$, SVC-FWE), ventral striatum ([$x = -9$, $y = 11$, $z = -11$], $Z = 5.05$, $k = 23$, $p < .001$, SVC-FWE, and [$x = 12$, $y = 14$, $z = -8$], $Z = 4.43$, $k = 18$, $p < .001$, SVC-FWE), and sgACC ([$x = -6$, $y = 14$, $z = -8$], $Z = 5.47$, $k = 32$, $p < .001$; and Self [$x = 6$, $y = 17$, $z = -8$], $Z = 4.60$, $k = 21$, $p = .001$; and [$x = 9$, $y = 8$, $z = -14$], $Z = 3.67$, $k = 2$, $p = .029$, SVC-FWE) (see Figure 2). These findings show that all regions of interest were involved in PE coding, in each condition.

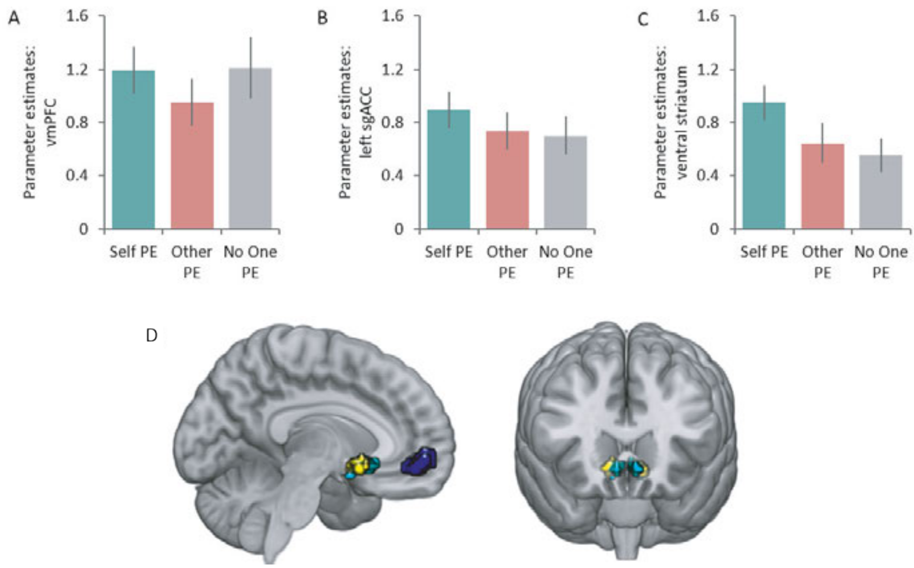


Figure 2. Common prediction error (PE) coding in three regions of interest. Shown are the responses to prediction errors for Self, Other, and No One in **(A)** the vmPFC, **(B)** left sgACC, and **(C)** ventral striatum. **(D)** Significant clusters of activation in the vmPFC (blue), sgACC (cyan), and ventral striatum (yellow). All images displayed at $p < .05$ FWE-SVC.

Next, we examined which brain regions responded more to PEs for Self than for Other by contrasting the Self condition against the Other condition (see Supplementary Table S4 for contrasts including the No One condition). The left ventral striatum was the only region to respond more strongly to PEs for Self ([x = 12, y = 11, z = -11], Z = 4.37, k = 9, $p < .001$, SVC-FWE; Figure 3). When examining effects of age we observed no linear or quadratic age-related differences in self-related PE coding. These findings indicate that the ventral striatum responds more to PEs for Self than for Others, and this effect did not differ across age.

We next identified regions that corresponded to PEs for others exclusively by contrasting the Other condition against the Self condition. No voxels in our ROIs responded more strongly to prosocial PEs than Self PEs. When adding age (linear and quadratic) to the model to examine whether age-differences were related to prosocial PE coding, we observed that the vmPFC increasingly responded to prosocial PEs with age ([x = -15, y = 50, z = 8], Z = 4.95, k = 45, p = .004, SVC-FWE; see Figure 4). No effects of quadratic age were observed. This shows that the vmPFC is increasingly involved in prosocial PE coding across adolescence.

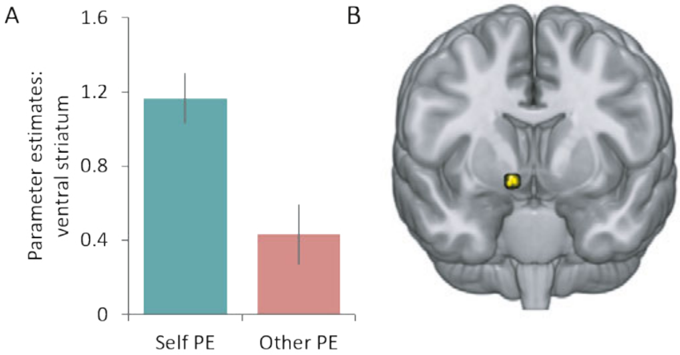


Figure 3. Ventral striatum response to prediction errors for Self versus Other. **(A)** Left ventral striatum [x=12, y=11, z=-11] response for Self PE and Other PE. **(B)** Overlay of the response for Self PE > Other PE in the left ventral striatum. All images displayed at $p < .05$ FWE-SVC.

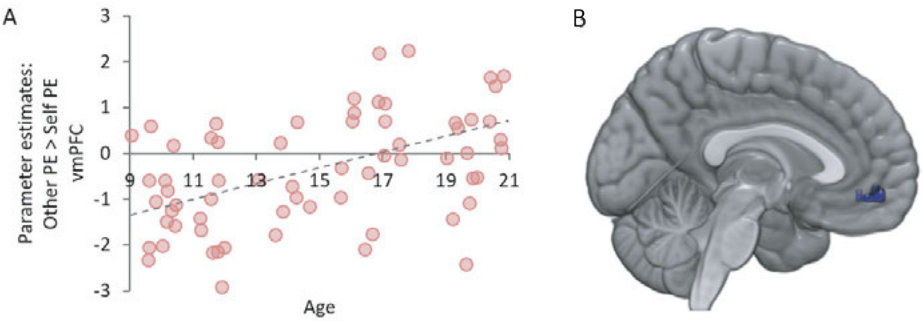


Figure 4. Linear age effects in responses to Other PE > Self PE in the vmPFC. **(A)** scatterplot showing the relation between age and activation in the vmPFC for Other PE > Self PE. Scatterplot is only presented for visualization. **(B)** Overlay of the response for Other PE > Self PE in the vmPFC [-15, 41, -11]. All images displayed at $p < .05$ FWE-SVC.

Links between cognitive empathy and learning for Others

Finally, we examined the link between cognitive empathy and prosocial learning. First, we assessed whether cognitive empathy related to performance for Other, while controlling for performance for Self. We observed that individuals with higher empathy ratings, showed better prosocial learning (r_s = .30, p = .01). Subsequently, we assessed whether cognitive empathy related to learning rate in the Other condition (controlled for learning rate in the Self condition). Results showed that individuals with higher empathy ratings had lower learning rates when learning for Others (cognitive empathy, r_s = -0.26, p = .027, see Figure 5B). Together, these findings indicate that individuals with more empathy show better learning performance, and integrate information more over trials when learning to benefit others. Finally, we assessed the relation between cognitive empathy and the prosocial PE coding in the vmPFC. For this purpose, we extracted the values of the Other PE > Self PE contrast in vmPFC that showed age-related change (see Figure 4). Results showed that greater Other vs Self-related PE activation in the vmPFC related to higher empathy scores (cognitive empathy, $r_s = .31$, $p = .007$).

To examine whether age-related differences in empathy or prosocial learning may influence these relations, we additionally included age in the partial correlation analysis. When additionally controlling for age, the relation between empathy and learning for others remained significant ($p = .029$), the relationship between empathy and learning rate became trend-level ($p = .06$), and the relation between empathy and prosocial PE coding was no longer significant ($p = .15$).

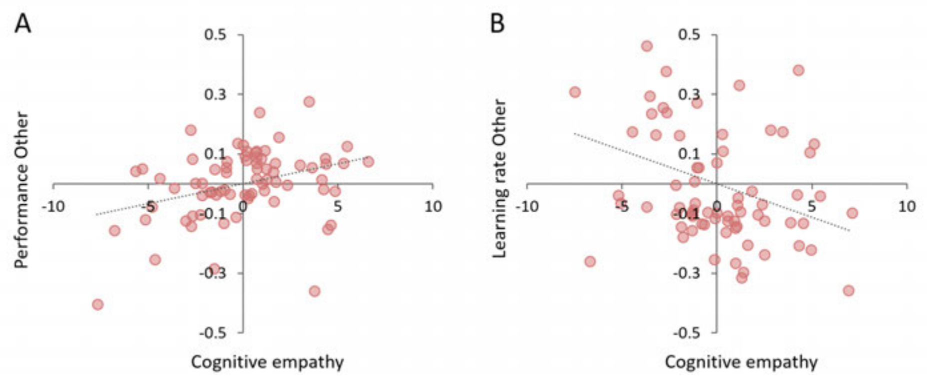


Figure 5. Relation of cognitive empathy with performance for Others and learning rate for Others. **(A)** Partial correlation plot showing that individuals with more cognitive empathy perform better for Others (controlled for performance for Self). **(B)** Partial correlation plot showing that individuals with more cognitive empathy have lower learning rates when learning for Others (controlled for learning rate for Self).

Discussion

This study examined the developmental trajectories of prosocial learning and self-related learning in an adolescent sample spanning ages 9-21 years. We examined the underlying mechanisms in this developmental sample by assessing the neural tracking of PEs during learning for self and others, and how individual differences in cognitive empathy relate to prosocial learning performance. To this end, participants played a two-choice probabilistic reinforcement learning task in which outcomes resulted in monetary consequences for themselves (Self) or an unknown other (Other; prosocial). Our results show improvements in learning for self and others, but the developmental trajectory of prosocial learning is more protracted compared to learning for self. PEs for self were related to activation in the left ventral striatum, which did not show age-related differences. On the other hand, vmPFC-related PE activation during prosocial learning increased with age, and related to individual differences in cognitive empathy. Together, these findings highlight that learning for self and others show different age-related patterns.

The main goal of this study was to examine age-related differences in prosocial learning. Behaviorally, we observed that it is not until mid-adolescence that participants learn similarly for themselves and others. These findings may suggest a self-bias that is stronger in younger ages (van der Aar et al., 2018), and that the motivation to learn for self and others increases with age. Neurally, we observe that a reward-related network including the ventral striatum, sgACC, and vmPFC respond significantly to PEs when learning for Self, Other, and No One. This conjunction presented the starting point for our interest in testing condition-specific learning effects. Contrary to Lockwood et al. (2016), who observed similar PE neural tracking values in the ventral striatum for learning for Self and Others in adults, we observed that PE neural tracking was stronger in the ventral striatum for Self than for Others. Recent reviews, however, suggest that the striatum is related to a range of computations that take place during social learning that could reflect both self-related and other-related learning (Joiner et al., 2017), or the difference between winning for self and others (Báez-Mendoza & Schultz, 2013). Therefore, one explanation for our findings could be related to the possible stronger self-focus or the greater focus on social comparisons reflected in the ventral striatum.

Learning for Others, compared to learning for Self, was associated with stronger activation in the vmPFC with age. Previous prosocial reinforcement learning studies have suggested that the vmPFC is also responsive to processing of self-related expected values (Sul et al., 2015), self-representation (Sui & Humphreys, 2017), or does not differentiate between self and other-related PEs (Lockwood et al., 2016). On the other hand, the vmPFC is suggested to respond to prosocial rewards in adults (Christopoulos & King-Casas, 2015), to others' outcome PEs (Burke et al., 2010), and to simulated others' reward PEs (Suzuki et al., 2012). Our findings extend these prior studies by showing that the ventral striatum and vmPFC code PEs both for self and others (see also Joiner et al., 2017). In this first developmental sample investigating prosocial learning, we observe a specificity for Self PEs in the ventral striatum and an increased specificity for prosocial PE coding in the vmPFC, in which across age prosocial (compared to self-related) PE elicit more activation. Alternatively, the pattern of age-related differences we observed for Other and Self-learning in the vmPFC may also support the perspective of a decreasing self-focus with age. For instance, previous work on self-concept development highlights that perspectives of others and self become more merged across development (van der Cruijsen et al., 2019). However, longitudinal studies are more powerful and essential for examining the true developmental trajectories of prosocial learning.

Besides the age-related differences in other-related learning, we observed that consistent with previous findings (Lockwood et al., 2016), individual differences in cognitive empathy were related to prosocial learning. Individuals with higher levels of empathy performed better for Others, integrated outcomes more over time (i.e., lower learning rates), and their vmPFC showed greater activation during prosocial PE coding. However, relations on cognitive empathy and prosocial PE coding in the brain were not robustly observed when controlling for age. This may indicate that it is hard to disentangle whether empathy or age drives prosocial PE coding. Also, age-related differences in brain activity during prosocial PE tracking may be explained by other social cognitive mechanisms than empathy. For instance, although there was no reciprocity or competition, participants may have been influenced by social inequality preferences, such as disliking to getting more (i.e., advantageous inequality aversion), or less (i.e., disadvantageous inequality aversion) than the other participant (Dawes et al., 2007; Fehr & Schmidt, 1999; Meuwese et al., 2015; Westhoff et al., 2020). Future studies could more explicitly assess several social-cognitive skills, strategies, and motivations along with a prosocial learning task to examine what behavioral mechanisms rely most on adolescents' prosocial learning.

Prior developmental studies on general reinforcement learning remained inconclusive about whether age-related differences were observed in PE neural tracking in the ventral striatum (Christakou et al., 2013; Cohen et al., 2010; Hauser et al., 2015; van den Bos, Cohen, et al., 2012). Here, age-related differences in PE coding for Self were not observed in the ventral striatum. In contrast to other studies (Cohen et al., 2010; Peters & Crone, 2017) we also did not find any quadratic age effects in learning or PE coding. This is possibly due to our narrower age range (9-21 y.o. instead of 8-30 y.o.), as another developmental study on learning also has not observed age-related changes in ventral striatum activity in a similar age range (van den Bos, Cohen, et al., 2012). Indeed, a recent review recommended using samples with wider age ranges, including children and adults, when examining quadratic age effects across adolescence (Li, 2017). It should be noted, however, that although we did not find age-effects in the ventral striatum, the behavioral learning performance for Self showed linear improvements with age. This could also indicate that other mechanisms than simple PE coding may be related to behavioral learning improvement over time within the current age range. For example, a prior study in young adults indicated that besides well-known model-free learning, another more sophisticated and flexible learning system is model-based learning. These two distinct computational strategies use different error signals which are computed in partially distinct brain areas (Gläscher et al., 2010). Moreover, it has been found that people may use different learning strategies, which show different neural activation patterns (Peters, Koolschijn, et al., 2014). Future studies are needed to assess whether age-related improvements in learning performance may be more strongly related to strategic learning differences.

We observed that, overall, learning rates decreased with age, and lower learning rates were related to better performance. These findings indicate that, with age, adolescents increasingly integrate information across trials, which was beneficial to their prosocial learning performance. Intriguingly, a recent aging study with a similar prosocial learning task observed that better learning performance was related to *higher* learning rates instead (Cutler et al., 2021; Lockwood et al., 2016). Besides the included age range in this study, a few differences in modeling and task structure may underlie this deviance. First, we allowed a wide range of beta-parameters. Since beta-parameters showed consistent age-related declines (see Supplementary Figure 2), and also relate to performance (see Supplementary materials) this may have influenced our learning rate estimations. Second, the task structure shows differences in reinforcement structure. Most profoundly we included gains and losses compared to gain and no-gains in previous prosocial learning studies. Possibly, losses may influence the updating of values across trials differently, although we did not find evidence that gains and losses were weighted differently in learning across development. Future studies should further examine the influence of reinforcement structures on observed age-related differences in reinforcement learning.

The current study had several limitations that can be addressed in future research. First, prosocial learning was restricted to unknown others, and participants did not meet these others. Although we circumvented the potential effects of reputational concerns, it may have been more salient to include a confederate, as used in previous studies on prosocial learning in which participants played for a stranger who they met prior to the experimental task (Lockwood et al., 2016; Sul et al., 2015). Second, it would be interesting if future research would extend the prosocial learning task to other beneficiaries. Previous studies have shown that prosocial behaviors and their neural correlates in adolescence strongly depend on the beneficiary (e.g., (Brandner et al., 2020; Schreuders et al., 2018; van de Groep et al., 2020; Westhoff et al., 2020). Future studies should further examine whether such differences between beneficiaries are also visible in prosocial *learning* and whether this affects the concurrent neural tracking of PEs. Third, the neural results for the No One condition showed an intermediate pattern between learning for Self and Others, which is difficult to interpret. Behavioral analyses showed that participants generally performed well in this condition (i.e., not significantly different from learning for Self), even though no monetary reinforcers were given depending on task performance. Although including the No One conditions in our contrasts of interest did not alter our main findings, this condition was possibly interpreted by participants in different ways, in which some participants were internally motivated to perform well (e.g., (Satterthwaite et al., 2012). Finally, in line with previous research we used a model with separate learning rates per condition (Lockwood et al., 2016). Using this established model, our results also revealed expected differences in learning rate between conditions. However, other studies also included comparison testing whether different learning rates or beta's are needed across different conditions (Cutler et al., 2021). Future studies may expand on these recent modeling procedure in prosocial learning in developmental and adult populations.

In conclusion, we found that prosocial learning showed age-related improvements across adolescence, suggesting a developmental shift from self-focus in early adolescence to self and other-focus in late adolescence and early adulthood (Crone & Fuligni, 2020). This developmental improvement was associated with stronger recruitment of the vmPFC for others compared to self. This study has implications for learning in social settings, such as educational contexts (Altikulaç et al., 2019), as well as for how children develop prosocial values when learning for unknown others. This study provides the first building blocks to understand age-related differences in how adolescents learn to benefit others.

Supplementary materials

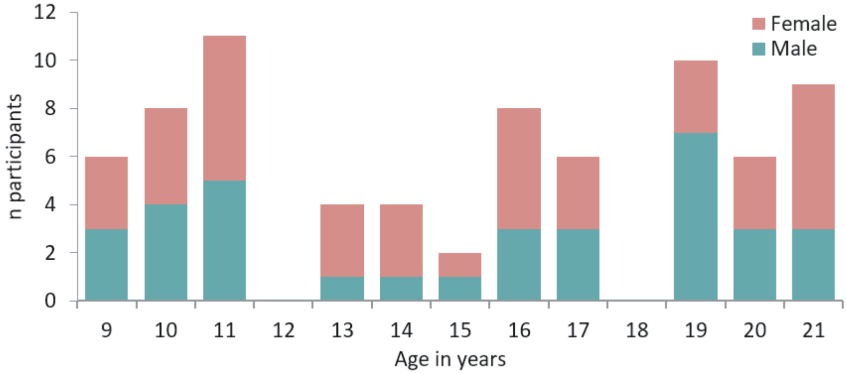


Figure S1. Number of participants across age per sex. In total, 74 participants were included (39 female, 35 male).

Beta parameter

The Beta parameter was examined as an index to what extent participants followed expected value in their choice behavior, and is also considered a parameter of decision noise. Higher values represent less decision noise here. Using a robust linear mixed effects model, we assessed effects of Condition and Age (linear) in beta parameters. We observed that with increasing age, decision noise decreased linearly (main effect of Age, $B = 2.9$, $p = .007$), indicating participants follow expected value more closely. Particularly beta parameters increased more strongly across age for Other than for Self (Other-Self; $B = 0.47$, $p < .001$), and did not differ significantly between No One and Other (No One – Other $p = .19$) and between No One and Self (No One – Self; $p = .19$)

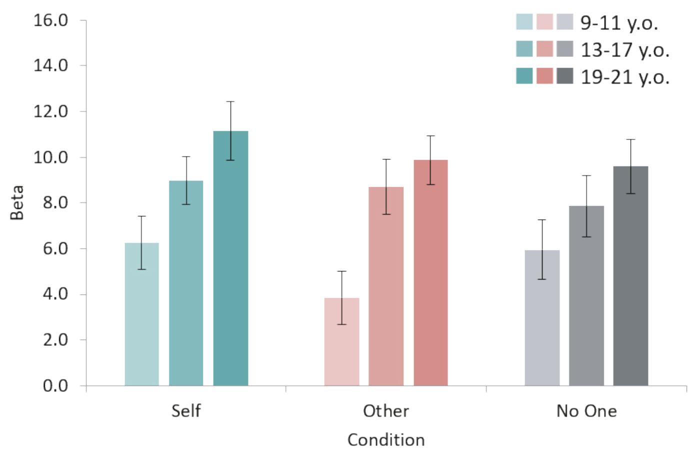


Figure S2. Beta parameter per condition per age cohort. Age is used as a continuous variable in all analyses, but is visualized as age cohorts for illustrative purposes and interpretability.

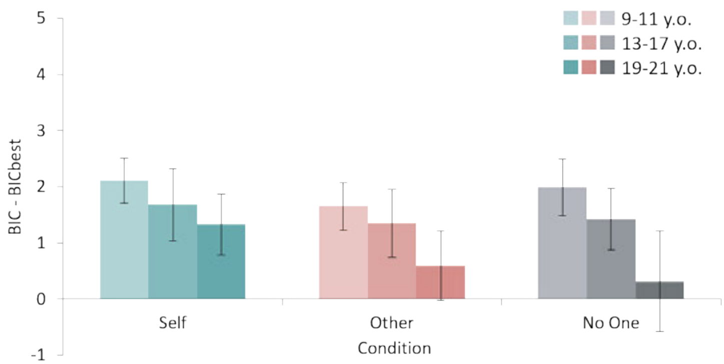


Figure S3. BIC values per condition per age cohort. Bars show BIC differences of the two-learning rate model (gain and loss) with the best model (one learning rate). Values on the y-axis indicate the difference between fit values (BIC values) for the two-learning rate model (gains and loss) and fit values for the one-learning rate model (the best model). BIC values were calculated per participant, and are shown separately per age cohort and per condition. For all age cohorts and all conditions a one-learning rate model is the best-fitting model. Lower bars indicate that the model fit of the one-learning rate model and two-learning rate model are more similar. For each condition, these BIC difference scores are not predicted by age (all *Ps* > .14). Error bars represent standard error of the mean.

Relations between performance, learning rates, and betas

We tested non-parametric correlations between performance, learning rates, and betas per condition. These show that lower learning rates in the Other condition are related to better performance for Other ($r_s(74) = -.38$, $p = .001$). Similarly, lower learning rates in the No One condition are related to better learning for No One ($r_s(74) = -.34$, $p = .003$, but learning rates in the Self condition are not significantly related to learning for Self ($r_s(74) = -.22$, $p = .056$). In addition, higher betas were strongly related to better performance in all conditions (Self, $r_s(74) = .91$, $p < .001$; Other $r_s(74) = .94$, $p < .001$; No One $r_s(74) = .89$, $p < .001$. Also, in all conditions, lower learning rates are related to higher betas (Self, $r_s(74) = -.37$, $p < .001$; Other, $r_s(74) = -.54$, $p < .001$; No One, $r_s(74) = -.48$, $p < .001$).

Figure S4. Learning rate and Beta parameter recovery. The correlation matrices represent the correlations between simulated and recovered **(A)** learning rates, and **(B)** beta values. Stronger colors show higher values and high values on the diagonal show parameters can be recovered.

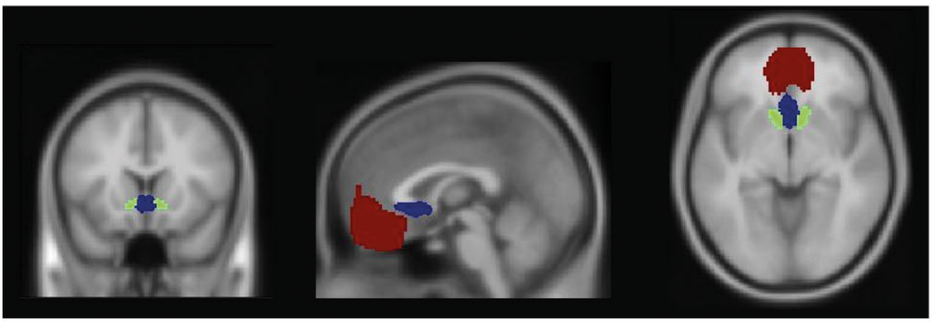


Figure S5. Regions of interest. Ventromedial prefrontal cortex (vmPFC; red), subgenual anterior cingulate cortex (sgACC; blue), and the ventral striatum (green).

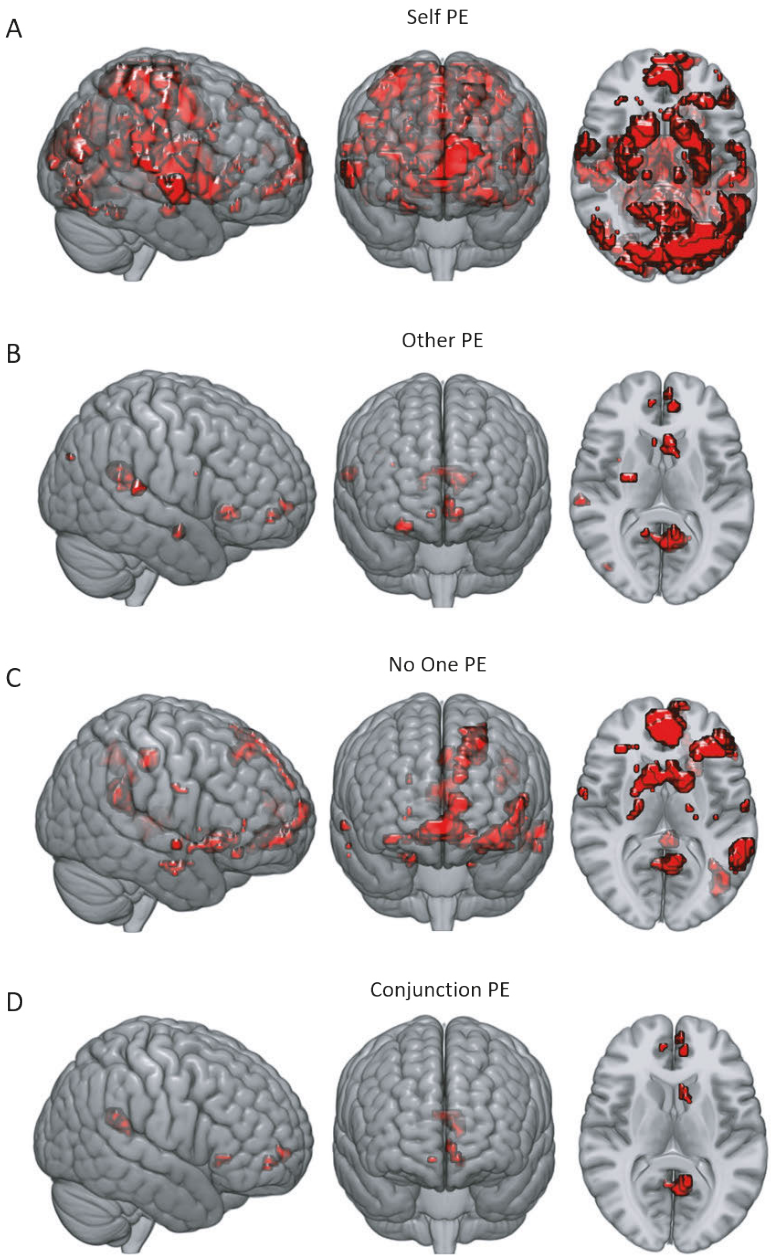


Figure S6. Whole brain responses for (A) Self PE, (B) Other PE, (C) No One PE, and (D) conjunction (common PE coding in all three conditions). All images displayed at $p < .05$ FWE, voxel level corrected.

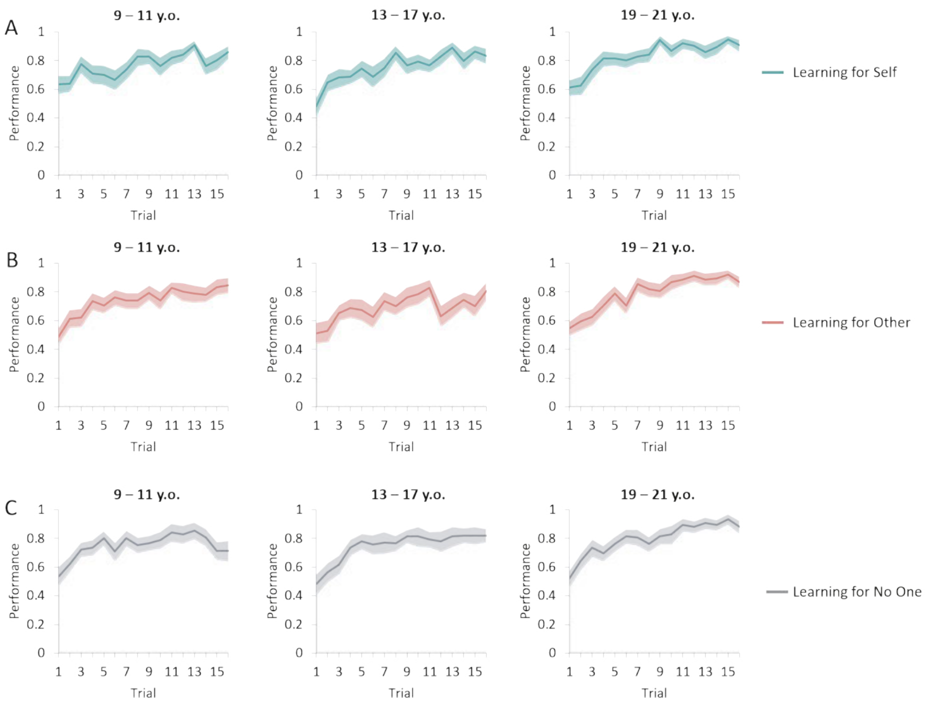


Figure S7. Learning across trials for (A) Self, (B) Others, and (C) No One, per age cohort. Note that for all analyses including age, we used age as a continuous variable. However, figures represent age per age cohorts instead for illustrative purposes and interpretability.

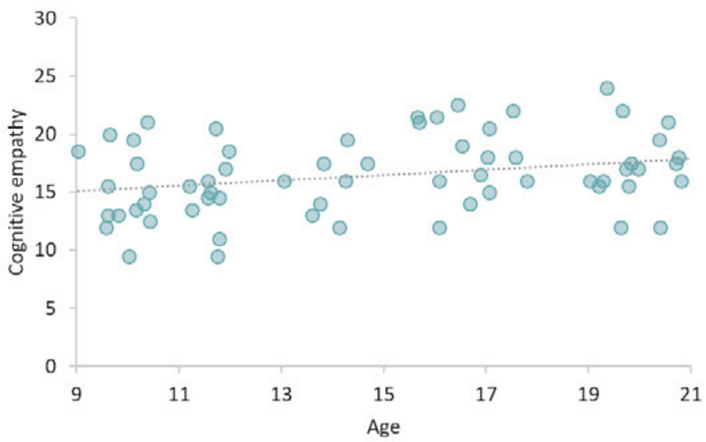


Figure S8. Cognitive empathy across age.

Table S1. Mean model parameters with prior distributions (M, SD), constraint, and 95% confidence intervals around the mean.

Model	**Parameter**	**Prior**	**Constraint**	**Mean**	**95% CI**
RL Self	α	β (1.2,1.2)	0 < α < 1	0.28	.24 – .32
	β	Gaussian (0,10)	−∞ ≤ β ≤ ∞	8.81	7.37 – 10.26
RL Other	α	β (1.2,1.2)	0 < α < 1	0.34	.29 – .39
	β	Gaussian (0,10)	−∞ ≤ β ≤ ∞	7.43	5.92 – 8.94
RL No One	α	β (1.2,1.2)	0 < α < 1	0.34	.29 – .39
	β	Gaussian (0,10)	−∞ ≤ β ≤ ∞	7.94	6.52 – 9.37

Table S2. Main effects of whole brain prediction error responses per condition, and common prediction error coding (conjunction).

Brain Region	*Peak voxel*					
	x	*y*	*z*	*k*	*t*	*z*
Main effect Self PE						
L Precental gyrus	-27	-25	61	6235	9.68	Inf
L precuneus	-3	-58	13		9.65	Inf
L Postcentral gyrus	-30	-34	64		9.03	Inf
L Putamen	-30	-13	4	481	9.52	Inf
L Putamen	-15	8	-11		8.20	7.65
R Caudate	12	11	-11	525	9.01	Inf
R Thalamus	30	-16	7		8.22	7.65
R Putamen	27	-7	10		8.04	7.52
L Superior frontal gyrus, medial	-9	65	19	515	7.25	6.85
L Superior frontal gyrus, medial	-12	58	7		6.93	6.58
L Superior frontal gyrus, medial	0	59	1		6.85	6.52
L Rolandic operculum	-48	-28	19	271	6.95	6.60
L Superior temporal gyrus	-60	-31	19		6.71	6.39
L Supramarginal gyrus	-60	-22	16		6.57	6.27
L Middle frontal gyrus, orbital part	-30	35	-14	50	6.73	6.41
L Thalamus	-12	-22	4	21	6.57	6.27
R Superior temporal gyrus	63	-1	-5	83	6.52	6.23
R Rolandic operculum	63	5	1		6.06	5.82
R Superior temporal gyrus	66	-7	4		5.29	5.13
L Inferior frontal gyrus,triangular part	-48	32	13	60	6.47	6.19
L Rolandic operculum	-54	-4	4	34	6.04	5.81
R Inferior temporal gyrus	51	-67	-11	46	5.76	5.55

Table S2. *Continued*

Brain Region	*Peak voxel* *x*	*y*	*z*	*k*	*t*	*z*
R Inferior temporal gyrus	51	-58	-20		5.41	5.23
R Inferior occipital gyrus	42	-76	-17		5.35	5.19
R Cerebellum	21	-52	-23	20	5.60	5.41
Main effect Other PE						
L Precuneus	-6	-61	13	103	6.54	6.25
L Calcarine fissure & surrounding cortex	-12	-55	10		6.19	5.94
L Olfactory cortex	-6	20	-11	32	6.29	6.02
R Hippocampus	30	-7	-20	17	5.66	5.46
R Superior temporal gyrus	63	-28	16	17	5.59	5.40
L Middle frontal gyrus, orbital part	-9	44	-11	12	5.58	5.39
Main effect No One PE						
L Middle frontal gyrus, orbital part	-3	50	-11	246	9.13	Inf
L Superior frontal gyrus, medial	-6	62	1		5.92	5.69
L Superior frontal gyrus, medial	-9	55	13		5.77	5.56
R Caudate	12	8	-11	173	7.64	7.19
L Olfactory cortex	-15	11	-14		6.72	6.40
L Olfactory cortex	-5	20	-11		6.19	5.93
L Inferior frontal gyrus, orbital part	-36	35	-14	182	7.60	7.15
L Middle frontal gyrus, orbital part	-24	32	-17		6.30	6.04
L Inferior frontal gyrus, triangular part	-45	32	7		5.99	5.75
L Middle temporal gyrus	-60	-43	-8	134	7.21	6.82
L Inferior temporal gyrus	-54	-52	-17		6.39	6.09
L Precuneus	-6	-55	16	120	7.16	6.78
L Calcarine fissure & surrounding cortex	-12	-52	7		5.88	5.66
L Median cingulate and paracingulate gyri	-3	-37	40	50	6.57	6.27
L Middle frontal gyrus	-24	32	49	172	6.56	6.26
L Middle frontal gyrus	-24	20	46		5.99	5.75
Superior frontal gyrus, medial	-12	59	28		5.64	5.45
L Angular gyrus	-42	-67	34	122	6.14	5.89
R Parahippocampal gyrus	18	-10	-26	16	5.63	5.43
R Parahippocampal gyrus	24	-19	-23		5.20	5.04
Conjunction						
L Precuneus	-6	-58	16	61	6.54	6.24
L Caudate	-6	14	-8	12	5.67	5.49

For all regions, FWE $p < .05$ voxel-level whole-brain corrected, and presented here with $k > 10$. PE = Prediction error; L = Left; R = Right; k =cluster extent. Names of the brain regions derived from the Automated Anatomical Labeling (AAL) atlas.

Table S3. Main effects of whole brain expected value responses per condition, and common expected value coding (conjunction).

Brain Region	*Peak voxel*					
	x	*y*	*z*	*k*	*t*	*z*
Main effect Self EV						
Precuneus	-15	-64	19	14	5.63	5.44
Main effect Other EV						
L Precuneus	-9	-61	19	53	6.01	5.77
R Middle frontal gyrus, orbital part	3	56	-5	23	5.51	5.32
Main effect No One EV						
L Middle temporal gyrus	-51	-13	-8	11	5.36	5.19
Conjunction*						
L Precuneus	-12	-58	13	140	4.28	4.18
L Precuneus	-12	-58	22		3.99	3.91
R Precuneus	6	-58	19		4.13	4.04

For all regions, FWE $p < .05$ voxel-level whole-brain corrected, and presented here with $k > 10$. PE = Prediction error; L = Left; R = Right; k =cluster extent. Names of the brain regions derived from the Automated Anatomical Labeling (AAL) atlas. *threshold $p < .001$

Table S4. Comparison of responses to prediction errors between conditions, in regions of interest (ventral striatum, sgACC, vmPFC).

Brain Region	*Peak voxel*					
	x	*y*	*z*	*k*	t	z
No One PE > Other PE						
Ventral striatum	12	8	-11	2	3.41	3.36
No One PE > Self PE						
No suprathreshold voxels						
Other PE > Self PE + No One PE						
No suprathreshold voxels						
Self PE + No One PE > Other PE						
Ventral striatum	12	8	-11	8	4.52	4.42
sgACC	9	8	-11	2	3.75	3.69
Self PE > Other PE + No One PE						
Ventral striatum	12	11	-11	3	3.34	3.30
No One PE > Self PE + Other PE						
No suprathreshold voxels						

Table S4. *Continued*

Brain Region	*Peak voxel*					
	x	*y*	*z*	*k*	t	z
Self PE + Other PE > No One PE						
No suprathreshold voxels						
Other PE + No One PE > Self PE						
No suprathreshold voxels						

For all regions, corrected at *p* < .05 FWE-SVC. PE = Prediction error; k =cluster extent. Names of the brain regions were based on the Automated Anatomical Labeling (AAL) atlas.

Table S5. Comparison of whole brain responses to prediction errors between conditions

Brain Region	*Peak voxel*					
	x	*y*	*z*	*k*	t	z
No One PE > Other PE						
No suprathreshold voxels						
No One PE > Self PE						
No suprathreshold voxels						
Other PE > Self PE + No One PE						
No suprathreshold voxels						
Self PE + No One PE > Other PE						
R Precuneus	15	-100	13	27	4.51	4.23
R Calcarine	18	-100	1		3.7	3.53
L Calcarine	-12	-103	-5	20	3.90	3.70
L Calcarine	-6	-103	1		3.73	3.55
L Postcentral	-36	-34	67	15	3.84	3.65
L Caudate	-12	-7	22	13	3.81	3.63
L Thalamus	-12	-16	13		3.68	3.51
Self PE > Other PE + No One PE						
L Occipital gyrus	-21	-88	22	2385	6.17	5.52
L Cerebellum	-33	-64	-20		5.02	4.64
R Occipital gyrus	24	-88	19		5.00	4.62
L Postcentral	-30	-37	67	701	5.31	4.87
L Precentral	-21	-25	58		4.85	4.50
R Precuneus	6	-43	58		4.63	4.32
R Putamen	33	-13	4	261	4.57	4.27
R putamen	30	-22	4		4.57	4.27

Table S5. *Continued*

Brain Region	*Peak voxel*					
	x	*y*	*z*	*k*	t	z
L Putamen	-30	-13	4	366	4.50	4.21
L Supramarginal gyrus	-57	-28	28		4.15	3.92
R Thalamus	3	-13	55	165	4.49	4.21
L Supplementary motor area	-3	-19	58		4.42	4.14
Median cingulate and paracingulate gyri	6	-1	43		4.13	3.90
R Middle frontal gyrus	36	50	31	22	4.13	3.90
R Supramarginal gyrus	45	-28	34	107	4.30	4.05
R Supramarginal gyrus	54	-28	37		4.02	3.81
R Superior frontal gyrus, dorsolateral	27	-10	70	33	4.25	4.00
L Superior temporal gyrus	-54	-4	4	24	4.04	3.83
L Putamen	-15	11	-11	11	4.02	3.81
R Precental gyrus	42	-10	58	25	3.89	3.69
R Precental gyrus	39	-10	49		3.83	3.64
R Thalamus	15	-22	1	10	3.75	3.57
No One PE > Self PE + Other PE						
No suprathreshold voxels						
Self PE + Other PE > No One PE						
R Precuneus	21	-64	25	99	4.63	4.32
R Calcarine fissure and surrounding cortex	21	-61	16		4.59	4.29
R Cuneus	15	-82	28		3.72	3.54
L Cuneus	-9	-82	22	75	4.33	4.07
L Cuneus	-15	-67	19		4.12	3.90
L Cuneus	-15	-82	31		3.29	3.17
R Insula	36	8	4	58	3.80	3.62
R Insula	36	2	16		3.61	3.46
R Supramarginal gyrus	66	-25	22	61	4.05	3.84
R Superior temporal gyrus	45	-34	22		3.58	3.57
R Supramarginal gyrus	54	-34	31		3.57	3.42
R Heschl gyrus	45	-25	13	18	3.92	3.72
L Middle occipital gyrus	-30	-76	22	12	3.67	3.50
L Middle temporal gyrus	-57	-67	4	10	3.62	3.46
Other PE + No One PE > Self PE						
No suprathreshold voxels						

For all regions, $p < .001$ voxel-level uncorrected, extent-threshold $k = 10$. Names of the brain regions were based on the Automated Anatomical Labeling (AAL) atlas.

Participant instructions

"Welcome! We are going to play a game in the scanner. In this game, you will see two pictures on the screen. You can win or lose points by choosing one of the pictures. If you win, you get +1 point, and if you lose, you get -1 point. But not all pictures are equally good…"

"With both pictures you can win and lose, but with one picture you will win more often, and with the other picture you will lose more often. Try to win as many points as possible! Note: it does not matter whether the picture is on the left or right side of the screen."

"To choose the left picture, you press the left button. To choose the right picture, you press the right button. At the end of the game, you will see how many points you won in total. Your points will be translated to real money using a formula. This amount of money will be paid out to you."

"You will play this game 3 times: for yourself, for another person, and for no one. On the screen, it says for whom you will be playing. Each time you should learn which of the two pictures on the screen is better. Sometimes you play for yourself. When you play for yourself, the gains will be paid out to you."

"Sometimes you play for another person. When you play for another person, the gains will be paid out to another player. This player is someone who participates in this experiment after you. This is a girl or a boy of your age. This person does not know that you are playing for him/her. So, he/she will receive the money you win for him/her without them knowing it is from you. This person will not play the game for you."

"Sometimes you play for no one. When you play for no one, your points don't count and no one will receive your gains."

"Try to respond on time. You will have about 2 seconds to make your choice. We will first do a practice run. Good luck!"

[24 Practice trials (8 per condition)]

"Well done! This was a practice run, so your points don't count yet. In the scanner, we will play the game for real, and you will see at the end of the game how many points you won for yourself and for the other person. Do you have any questions left?"

6

Chapter 6

Summary and General Discussion

Summary

The overarching goal of this thesis was to examine the behavioral, computational, and neural mechanisms underlying social learning in adolescence. The first aim was to examine developmental patterns across adolescence of two forms of social learning: (1) learning *about* other people, specifically, whether they are (un)cooperative and (un)trustworthy, and (2) learning *for* other people (prosocial learning) to know what actions may benefit or help others. I made use of multiple experimental paradigms based on well-known economic games and/or probabilistic reinforcement learning paradigms to assess these forms of social learning. A second aim was to examine underlying mechanisms and factors that account for age-related and individual differences in social learning. Applying computational modeling and functional neuroimaging as additional tools contributed to a better understanding of the underlying mechanisms and how these develop across adolescence. In this final chapter, first, the main findings of each chapter are briefly summarized. The summary is followed by a general discussion, including implications of the findings and recommendations for future research.

Learning about others' behavior in adolescence

In the first empirical chapter (**chapter 2**), I examined developmental patterns and mechanisms of learning *about* others. Specifically, in a large adolescent sample spanning a broad age range (*N* = 244, 8-23 years), I examined adolescents' ability to learn about and adjust to others that differed in their levels of cooperation. Here, I focused on two different key types of cooperative behaviors – trust and coordination – for which I conceived two games. These games consisted of multiple 1-shot economic games forming a probabilistic reinforcement learning task. Participants encountered anonymous peers who showed either low or high levels of cooperative behavior. Over trials, participants could learn about these others, and by adjusting their own choice behavior (cooperate vs. not cooperate), they could maximize their outcome. In the game involving trust ('trust game'), participants could learn to trust trustworthy others and not trust untrustworthy others. In the game involving coordination ('coordination game'), participants maximized their outcomes by choosing to accept a disadvantage (i.e., cooperative behavior) when they encountered uncooperative others, and to accept an advantage (i.e., uncooperative behavior) when they encountered cooperative others.

The first aim of this study was to investigate the age-related differences in learning about and adjust to cooperative and uncooperative others in adolescence. In both games, adolescents' social learning abilities showed a developmental asymmetry: adolescents adjusted well from an early age when this required *uncooperative* behavior (i.e., not trusting, accepting an advantage). Yet, learning about others improved profoundly in early-mid adolescence when this required *cooperative* behavior (i.e., trusting, accepting a disadvantage).

Next, I examined the effects of inequality aversion (disliking being ahead or behind), prior expectations about others' behavior, and the updating of expectations about others (i.e., learning rates) as potential underlying mechanisms. Combining behavioral analyses with computational modeling revealed that age-related improvements in social learning were partly explained by age-related decreases in inequality aversion. That is, younger adolescents disliked being behind more than older adolescents and this hampered their social learning, particularly when it required cooperative behaviors. Moreover, although prior expectations were not related to choice behavior in the games, in the *updating of expectations* (i.e., learning rates), there were age-related differences: in early-mid adolescents, the learning rates did not decrease (much) across trials. This indicated that they did not form stable expectations over time, but instead kept updating their expectations of others throughout the games. From mid-adolescence onwards, participants more effectively integrated outcomes over time, and consequently formed stable expectations of others which would not quickly be overridden by a single experience that did not match built-up expectations. Together, this chapter's findings point to early-mid adolescence as a developmental window for a rapid change in adaptive social learning, with improvements especially in the cooperative domain.

Learning (flexibly) about others' trustworthiness in adolescence

The experimental study in **chapter 3** extended on the study and findings from chapter 2 to further study how adolescents learn about and adjust to others' trustworthiness. As such, I used the trust game from chapter 2 in an adolescent sample with a broad age range (N = 157, 10-24 years). Additionally, a non-social variant of the trust game was included to assess whether trust learning patterns were specific to learning in a social learning context. Moreover, I studied participants' ability to flexibly adjust trusting behavior by including a reversal learning manipulation in which the trust behavior of the other players reversed unannouncedly from trustworthy to untrustworthy, and vice versa.

In line with the findings from chapter 2, participants of all ages found it harder to learn about and adjust to trustworthy than to untrustworthy others. However, contrary to the findings of chapter 2, learning about trustworthy and untrustworthy others showed similar linear age-related improvements across adolescence. The reversal learning results showed that adolescents' abilities to learn who was no longer trustworthy (switch to untrustworthy) were stable across age. In contrast, with age, adolescents became better at learning who was no longer untrustworthy (switch to trustworthy). This age effect in social reversal learning indicates increasing flexibility in social trust learning from mid-adolescence, which seems especially pronounced for learning in the cooperative domain. The trust (reversal) learning patterns were similar for social and non-social trust learning, suggesting that social and non-social trust learning processes are either at least partly overlapping or, alternatively, distinct neurocognitive subprocesses may have resulted in similar behavioral outcomes (Morton, 2010).

Finally, I assessed adolescents' reported parenting practices as a potential factor influencing social (reversal) learning abilities. As highlighted in the introduction, adolescence is a period in which peers play an important role. However, our view of the world and our expectations of others could also be influenced by our home environment. For instance, previous research has shown that individuals who grow up in households with mostly negative parenting practices (e.g., expressing negative emotions, handling roughly), physical and emotional neglect, or even maltreatment (e.g., physical and emotional abuse), have an increased risk on, among others thing, impaired social functioning (Gobin & Freyd, 2014; McCrory & Viding, 2015; Overbeek et al., 2020). However, it was yet unknown whether environmental variables such as parenting practices also affect adolescent's social (reversal) learning abilities. This study showed that adolescents who reported having experienced more negative parental practices (specifically, poorer parental monitoring) showed reduced abilities in flexibly learning who was no longer trustworthy (switch to untrustworthy). Specifically, they showed too much trust towards others who had become untrustworthy.

Together, these results point to adolescence as a period for developing adaptive social trust learning abilities, which become increasingly flexible from mid-adolescence onward. Yet, one's family environment may impact adolescent's adaptive social learning abilities.

Effects of prior beliefs on trust behavior

In **chapter 4**, I further investigated adaptive trust behavior in adolescence and assessed the underlying cognitive processes involved in trusting behavior. When we decide to trust someone, there is uncertainty about whether they will reciprocate that trust. This uncertainty can often be reduced by gathering information, for example, about a person's history of trustworthiness. An essential component of well-adjusted social behavior is the ability to *update* our beliefs about others' trustworthiness based on gathered information. In this empirical chapter, I examined in a large adolescent sample (*N* = 157, 10-24 years, same sample as in chapter 3), how and how much information adolescents sample about others' trustworthiness for deciding whether or not to trust them, and how they use this information to update their beliefs about these others' trustworthiness. Using a trust sampling paradigm, participants could gather (sample) information about unknown peers' past reciprocation behavior before they decided to trust them or not. Compared to chapters 2 and 3, where the trustworthiness levels of others were merely trustworthy or untrustworthy, there were multiple trust levels ranging from always trustworthy to always untrustworthy.

Behavioral analyses showed, in line with findings from chapter 2 and 3, that older adolescents trusted trustworthy others more often than younger adolescents. Moreover, with age, adolescents sampled information about others more adaptively, as older adolescents especially sampled more information when the sampled information was rather inconsistent (i.e., around 50% trustworthy) compared to when the sampled information was consistent (e.g., around 100% trustworthy or 100% untrustworthy). Additionally, a Bayesian computational modeling approach was used to examine the processes underlying trust information sampling behavior and its age-related differences. This procedure revealed that the amount of information adolescents sampled for deciding whether to trust was determined by their prior beliefs about trustees' trustworthiness (before any information was sampled). Specifically, compared to older participants, younger participants expected others to be somewhat less trustworthy. The most important age-related difference was found for participants' *uncertainty* about prior beliefs, which refers to how much variation in trustworthiness they expected to encounter. This uncertainty strongly increased from early-to-mid adolescence, leading adolescents to rely less on their prior beliefs and more on the sampled information. As a result, younger adolescents sampled more than older adolescents when the trustees were trustworthy, as the sampled information did not match the younger participants' expectations. In addition, there was an age-related increase from early to mid-adolescence in how often participants trusted highly trustworthy trustees. Thus, the older adolescents based their trusting decisions more on the gathered information than on their prior beliefs.

Thus, these findings point to early-to-mid adolescence as a developmental phase in which adolescents become more open-minded about possible individual differences in other people's trustworthiness, which allows them to flexibly learn that some people are highly trustworthy while others are not.

Prosocial learning in adolescence

In **chapter 5**, I investigated another type of social learning: prosocial learning. Here, I presented an experimental fMRI study investigating developmental patterns and underlying mechanisms of prosocial learning across adolescence. In an adolescent sample aged 9-21 years (N = 74), I used a two-choice probabilistic reinforcement learning task that had previously been used in adult studies (Lockwood et al., 2016; Sul et al., 2015). In this task, participants were instructed to make a series of decisions between two pictures; over trials, they could learn which of the two was associated with the high versus low probability of winning a monetary reward. They played different conditions of the task: they could learn to obtain positive outcomes either for an unknown other participant who could not reciprocate (Other; prosocial), or for themselves (Self). As such, with this task I measured prosocial learning and distinguished it from self-benefitting learning.

Behavioral analyses showed that adolescents between 9 and 21 years old were able to learn to obtain rewards for themselves and others, but the most pronounced age-related improvement in learning performance was observed for prosocial learning. Additionally, for unraveling underlying mechanisms of prosocial learning, a reinforcement learning computational model was applied to the behavioral data, yielding learning rates and prediction errors. Learning rates, indicating how strongly expectations are updated after an unexpected outcome, were lower for learning for self than for prosocial learning. Moreover, the age-related change in learning rates was most pronounced for prosocial learning compared to self-benefitting learning. By combining computational modeling with functional neuroimaging, I was able to track the prosocial learning signals (i.e., prediction errors) in the brain. In line with previous adult and developmental research (Cohen et al., 2010; Davidow et al., 2016; Hauser et al., 2015; Joiner et al., 2017; Jones et al., 2014; Lockwood & Klein-Flügge, 2020; Ruff & Fehr, 2014), prediction errors for self were observed in the ventral striatum, yet no age-related differences were observed. On the other hand, prediction error coding for prosocial learning was related to activation in the vmPFC. This vmPFC-related prediction error activation during prosocial learning increased with age, and related to individual differences in cognitive empathy.

Together, the findings from this chapter show that prosocial learning abilities improve early-to-mid adolescence on both a behavioral, computational, and neural level. The various indices provide a complementary perspective showing that especially learning for others undergoes developmental transitions, consistent with the conclusions of the previous chapters showing that age-related differences are most pronounced for other-oriented behaviors.

General discussion

In this section, I highlight several discussion points that result from the work in this thesis. First, I discuss that the findings in this thesis converge to early-to-mid adolescence as a key developmental period in adaptive social learning and well-adjusted social behavior, especially with regard to cooperative behaviors such as trusting others. Moreover, I discuss the advances of the application of computational modeling to a developmental perspective. Finally, I reflect on future directions that will move the field of developmental social neuroscience forward.

Adolescence as a key developmental period for developing well-adjusted social behaviors

In the empirical chapters of this thesis, I investigated age-related changes in learning about and learning for others in adolescence. To study these age-related changes, I collected and analyzed data from broad age ranges covering the adolescent period, which enabled studying linear and non-linear (i.e., quadratic) effects of age (Li, 2017). In each chapter, results showed that early-mid adolescence is a developmental window that shows age-related improvements in adaptive social behaviors, more so than for non-social learning (e.g., learning that affects only self). For example, I observed rapid improvements from early adolescence in developing adaptive social learning when these required cooperative behaviors (chapter 2). Moreover, I demonstrated that adolescents showed monotonic increases in flexibility in learning whom to trust (chapter 3), and accelerated increases in the uncertainty of prior beliefs about others, which affected their information sampling and subsequent trust decisions (chapter 4). Finally, adolescents' prosocial learning abilities showed stronger improvements with age than self-benefitting learning (chapter 5). Besides these age-related changes in behavior, I also showed age-related increases in activity in the vmPFC for prediction errors during prosocial learning, whereas prediction errors when learning for self (ventral striatum) were already in place before adolescence (chapter 5).

Thus, this thesis shows an improvement in adaptive social learning in adolescence. Such improvements, especially in the social domain, are particularly relevant in a developmental phase such as adolescence. That is, adolescence is characterized by changes in social relations, such as building new friendships, and engaging in a diversity of social environments including school, sports clubs, and social gatherings (Fuligni, 2019). Therefore, adolescents may have a specific advantage to showing well-adjusted social behaviors, such as adaptive social learning.

Moreover, this thesis shows that age-related improvements in social behaviors are mostly observed, or are strongest, in the *cooperative* domain, such as learning whom to trust compared to learning whom not to trust (chapter 2 and 3), and learning how to help or benefit others (prosocial learning) compared to learning to benefit ourselves (chapter 5). This is in line with previous research showing that other-oriented behavior – such as cooperative behaviors – improves across adolescence (Crone & Fuligni, 2020). It is suggested that adolescence is an important period for creating the right balance between needs of self and others, in order to build secure interpersonal relations and to become contributing members of society (Crone & Fuligni, 2020; Fuligni, 2019). This was also demonstrated in chapter 2, in which age-related decreases in inequality aversion (disliking having less than others) were related to age-related improvements in social learning abilities. Particularly, older adolescents did not as much dislike to have less than others, which was associated with becoming better at learning about and adjusting to others when it involved showing cooperative behaviors. Together, the findings in the current thesis are in line with the hypothesis that with increasing age, we become 'less selfish' and we are better able to coordinate with others for collective welfare, even though this may not be equally beneficial for oneself as for the other.

It should be noted that the mentioned age-effects in this thesis' empirical chapters result from cross-sectional studies. Therefore, it is necessary that the reported developmental patterns should be further investigated in studies with a longitudinal design. Longitudinal studies are more powerful and essential for examining the true developmental trajectories and within-person change (Crone & Elzinga, 2015). A longitudinal setup would moreover allow for investigating the stability in social relations, and how these relate to social learning (Schreuders, Braams, et al., 2021). Therefore, future studies would benefit from following participants with similar learning paradigms over multiple time points (Telzer et al., 2018).

Using computational modeling for studying social behavior in development

In this thesis, I combined methods and insights from different research fields, such as developmental psychology, social psychology, behavioral economics, and neuroscience. This multidisciplinary perspective is necessary to advance the field and to better understand the development of adaptive social behavior. Moreover, the application of computational modeling to study social learning in a developmental sample was a relatively innovative approach. That is, only in the last decade researchers have started to apply computational modeling to investigate learning from reinforcement in children and adolescents (Nussenbaum & Hartley, 2019), and the majority of these studies have investigated learning from feedback in non-social contexts. Yet, applying computational models to *social* learning data has been done merely in adult studies (Joiner et al., 2017; Lockwood et al., 2020; Olsson et al., 2020), and thus the computational underpinnings of social learning across development is relatively unexplored.

By applying computational modeling to developmental samples, the empirical chapters of this thesis have provided several insights. First, it revealed the role of learning rates on developmental patterns of social learning abilities. Specifically, I observed that learning rates show age-related decreases for learning *about* others (chapter 2) and learning *for* others (chapter 5). Here, these age-related decreases in learning rates were related to age-related improvements in social learning abilities. This suggests that it was more optimal to incorporate feedback over a longer time frame in these learning tasks. However, one cannot conclude that in every (social) learning context there will be age-related decreases in learning rates across adolescence, as each learning context may require a different 'optimal' learning rate (Zhang et al., 2020). That is, for more stable learning environments, a lower learning rate may be more appropriate. In contrast, a higher learning rate would be more efficient for learning in more volatile or unpredictable environments. This thesis' chapters had relatively stable social learning environments; future studies are needed to investigate whether people have different learning parameters across several learning contexts differing in the level of volatility.

Second, applying computational models to adolescents' information sampling behavior in chapter 4 enabled assessing adolescents' prior beliefs, and uncertainty of these prior beliefs, and how these were involved in trust decisions. Instead of explicitly asking participants via self-reports, these prior beliefs could be extracted as latent variables from behavior. Self-reports may have several biases, such as social-desirability bias (Althubaiti, 2016), or may falsely induce age effects in a developmental sample. Therefore, computational modeling is a powerful way to gain additional information on the (development of) underlying cognitive processes in social behavior (see also van den Bos et al., 2018).

Finally, the computational models enabled precise tracking of learning signals in the brain during prosocial learning (chapter 5). Former (developmental) studies investigating the neural underpinnings of learning examined neural activation at the time of outcome by contrasting losses and gains. However, using prediction errors as parametric values makes it possible to track how brain activation covaries with the model computations on a trial-by-trial basis. Several recent studies in adults have applied such an approach which yielded new insights into human social behavior (see Lockwood & Klein-Flügge (2020) for an overview). Therefore, future developmental studies investigating learning should aim to use such learning parameters in their fMRI analyses.

Taken together, I encourage future studies also to apply computational modeling to investigate underlying latent mechanisms of social behaviors. However, when applying computational models in developmental samples with broad age ranges, one should be aware that different model variants should be compared. That is, in chapters 2, 4, and 5 of the current thesis, multiple computational models were applied to the behavioral data and the model fits were compared across ages. In these studies, choice behavior was equivalently well described by the same model across the entire age range, suggesting that the same processes underly behavior from early-to-late adolescence. Similarly, a previous study investigating reinforcement learning in a sample of 8-22 year-olds applied computational modeling and found the same best-fitting model across all ages (van den Bos, Cohen, et al., 2012). However, some studies found distinct best-fitting models across development (e.g., (Decker et al., 2015; Palminteri et al., 2016; Worthy et al., 2014). For example, a study examined computational strategies underlying learning from reward or punishment, and learning from counterfactual feedback for adolescents and adults (Palminteri et al., 2016). It was found that adolescents' and adults' learning behavior were best described by distinct models, suggesting that the underlying computational strategies in these tasks changed across development. These deviances between studies (i.e., same or different models/strategies for different ages) suggest that learning processes may be context-dependent. Therefore, future studies applying computational modeling in a developmental sample should avoid assuming that the same models and thus computational processes apply to both adolescents and adults.

Future directions

The findings in the current thesis provide a starting point for future studies to address several outstanding questions. In this section, I discuss ideas for extending current research methods and introduce new research approaches that could help to increase our understanding of well-adjusted social behaviors and how these develop.

Assessing developmental patterns of social behaviors in adolescence

One of the aims of the current thesis was to assess developmental patterns of social learning in adolescence. To this end, for each empirical chapter, I collected data from samples spanning broad age ranges and examined the age-related changes in, for example, (pro)social learning performance. However, it is not unlikely that developmental trajectories in social learning are not (solely) determined by chronological age; additionally, development may be influenced by puberty. Puberty is characterized by sharp rises in gonadal hormones, such as testosterone and estradiol, which are thought to influence the developing brain (Goddings et al., 2019; Peper & Dahl, 2013). Prior research has shown that pubertal stage and hormone levels are associated with cortical and subcortical volumes, as well as structural and functional brain connectivity. For example, a comprehensive longitudinal neuroimaging study investigated the development of functional connectivity between subcortical and cortical brain structures across adolescence (van Duijvenvoorde et al., 2019). Findings showed that for specific connections, pubertal development described developmental change better than chronological age. Also, with regard to structural brain development, it has been found that pubertal maturation has additional explanatory value above age (Herting & Sowell, 2017; Wierenga et al., 2018). Finally, the rise in pubertal hormones is particularly associated with reward-related areas such as the striatum (Braams et al., 2015; van Duijvenvoorde et al., 2014), and pubertal development was a better predictor of reward-related brain activation over and above age (Pfeifer et al., 2013). It has, moreover, been suggested that particularly puberty increases flexible learning and quick adaptation to novel social contexts in adolescence (Crone & Dahl, 2012). Therefore, it is not unlikely that puberty may be a better predictor than chronological age also for developing adaptive social learning skills.

Development in context

Development is a complex process that is influenced by multiple mechanisms, and plausibly not only by age and puberty, but also by external environmental factors. It has been shown that external factors, such as early life stress and adverse childhood experiences may have detrimental effects on trajectories of neurocognitive development (Sheridan & McLaughlin, 2014). That is, adverse childhood experiences can impact structural and functional brain development, and can moreover impact social and emotional development. For example, previous research has shown that social and emotional development in bullied and chronically rejected children is negatively affected (Asscheman et al., 2019; Will et al., 2016). Besides, also reward learning is shown to be impacted by childhood adversity (Dennison et al., 2019). For instance, adolescents who had been exposed to early adversity in the form of physical abuse showed impaired associative learning, compared to controls (Hanson et al., 2017). These findings indicate that external environmental factors may also impact the development of social learning. Therefore, for future research it is thus important to move beyond considering simple age-related changes, and additionally incorporate the influence of other developmental processes, such as puberty or key experiences, when studying social development.

Methodological Advances

In the current thesis, I aimed to incorporate a solid methodological setup to investigate the development and underlying mechanisms of social learning. That is, in chapters 2-4, I focused on behavioral and computational analyses for assessing trust (learning), and in chapter 5, I examined prosocial learning by extending behavioral and computational analyses with fMRI analyses. However, other methods may also inform the questions related to social learning, especially novel neuroimaging techniques. One such approach is psychophysiological interaction (PPI), a method to assess task-based functional connectivity (Friston, 1994), which may reveal which brain areas interact during certain events. As such, it provides additional information on the neural circuitry involved in social decision-making and learning. PPI has been applied in some developmental studies (e.g., (van den Bos et al., 2013; van Duijvenvoorde et al., 2014), but more developmental neuroimaging studies could benefit from applying this technique.

An additional valuable technique that could be particularly beneficial in this line of research is representational similarity analysis (RSA) (Kriegeskorte et al., 2008). This technique allows assessing the BOLD signal in a trial-by-trial manner to quantify the (dis)similarity between stimuli or trials. Although this technique has revealed promising advances in the field of fear learning (Undeger et al., 2020; Visser et al., 2013, 2015), it has not been used much in social neuroscience (Popal et al., 2019). However, a recent study using RSA demonstrated the added value for social neuroscience. This study investigated decision strategies of adults when deciding to reciprocate someone's trust. Using RSA, it was able to reveal that people had different decision strategies, which were associated with distinct brain patterns (van Baar et al., 2019). However, especially in developmental (social) neuroscience, the application of RSA has been scarce. A recent developmental neuroimaging study examined adolescents and their mothers. By using RSA, it could reveal that adolescents' neural representations for self and their family were related to family relationship quality (Lee et al., 2017). Specifically, neural representations for harm to self and to their family were more similar when the family relationship quality was better. These examples reveal that RSA may reveal valuable insights in developmental social neuroscience, and I encourage future research on social learning to apply this technique.

Although several methodological recommendations remain to be further explored and applied in developmental neuroscience, it has to be acknowledged that already many advanced methodologies have been embraced in recent years. Strong methodological setups are essential to advance the field further, but are also complex and therefore require even stronger interdisciplinary approaches. Consequently, a faster transitioning towards a team science approach in academia, in which collaborators with different expertise use their strengths to supplement each other, is more necessary than ever.

Ecological validity and generalizability of findings

The paradigms in chapters 2-4 were based on well-known economic games where participants interacted with other players. Whereas many previous studies investigating social interactions used paradigms that were not interactive (e.g., observing others' faces or mental states; 'spectatorial approach'), I used a two-directional approach in which two players make choices, which influence each other's rewards (Camerer & Mobbs, 2017). This latter approach is acknowledged to be an important aspect of paradigms investigating social behavior (Camerer & Mobbs, 2017). The advantage of such paradigms is that they allow for studying complex social behaviors in a simple and controlled way, making them moreover suitable for neuroimaging experiments. However, despite the two-directional approach, in this thesis' controlled experimental setups the social interactions are far less complex than in real-life social interactions. For example, participants did not interact face-to-face with their interaction partners. However, in real-life social interactions, other factors such as facial features also play a fundamental role. For example, a recent comprehensive study showed that trust decisions were implicitly affected by the trustees' pupil size, with more dilated pupil size resulting in more reciprocated trust (Kret & De Dreu, 2019). Moreover, when the pupils of interaction partners simultaneously dilated (pupil mimicry), trust decisions were promoted (Prochazkova et al., 2018).

Another discrepancy from real-life social interactions concerns the targets. That is, people's social life involves many different social interactions with familiar others, such as interactions with classroom peers, teachers, parents, siblings, or neighborhood peers. Previous research has shown that different processes may be involved in interactions with familiar others. For example, adolescents showed distinct neural activation patterns during vicarious rewards for their father and mother compared to strangers (Brandner et al., 2021). Moreover, a behavioral study found that with increasing age, adolescents trusted friends more than disliked others and strangers (Güroğlu et al., 2014). Besides, experienced interactions with familiar others could also affect the social development of children and adolescents. Therefore, future studies on social learning would benefit from including different targets to increase understanding of the complexity of social behaviors.

Previous studies have shown that behaviors in economic games relate to actual behavior or attitudes in real-life situations (Camerer, 2003). However, it is often difficult to translate research findings to real-life learning situations due to the lack of naturalistic stimuli or because the social interactions are simplified too much compared to real complex behaviors (Atteveldt et al., 2018; Camerer & Mobbs, 2017). A fruitful new research approach to improve the ecological validity of neuroscientific research on social learning, could be the use of portable neuroimaging techniques (Atteveldt et al., 2018). This novel technology can for example be applied in the classroom while the children are interacting with each other. As such, brain activity can be measured during real-life learning situations, which may ease the translation to daily learning situations.

Moreover, an interesting avenue for future research could be to implicate virtual reality (VR) for studying social interactions and social learning. With VR, it is possible to mimic social situations while having experimental control. In clinical practice, virtual reality has already proven to be a valuable technique (Meyerbröker, 2021). For example, former intensive care patients often have post-traumatic stress disorder or anxiety due to hospitalization, and it has been shown that a VR intervention can improve psychological wellbeing (Vlake et al., 2021). Recently, the application of interactive virtual reality has also been introduced in the field of psychology. A recent pilot study (Verhoef et al., 2021) created a virtual classroom using VR to study social interactions which were standardized yet emotionally engaging. This study showed that it was a promising method to assess children's aggressive social information processing. The application of VR could also be extended to a social learning context, and may play a role in interventions targeted at improving social behaviors.

Generalizability of findings across the globe

Overall, the findings in this thesis are in line and/or complement each other. However, some effects seem to be sample-specific. For example, regarding trust learning, I observed a developmental asymmetry in chapter 2, with learning to adjust uncooperative behaviors being rather stable across age, whereas learning to adjust cooperative behaviors showing improvements across age. In chapter 3, however, we did not replicate this asymmetry in trust learning (yet, trust *reversal* learning did show a similar developmental asymmetry). As the learning tasks used in these chapters were nearly identical, this deviation could be explained by sample specifics. That is, for the study in chapter 2, data collection took place at school and required minimal effort from participants and their caregivers. This setup resulted in a relatively heterogeneous sample with regard to, e.g., SES and educational level. For the study from chapter 3, participation required more effort because participants and a caregiver (in the case of minors) were invited to the lab, which has contributed to a relatively homogeneous sample with regard to e.g., SES and educational level. In the latter study, this data collection setup may have resulted in a sampling bias affecting the observed developmental patterns. That is, as in most conducted research in psychology and neuroscience, the included participants in this thesis are from a Western, educated, industrialized, rich, and democratic (WEIRD) society. However, someone's culture, ethnicity, and SES plausibly affect social behaviors and thus the developmental patterns. For example, studies investigating social behaviors in multiple cultures have shown diverging developmental patterns across cultures for prosocial behavior (House et al., 2020) and fairness norms (Blake et al., 2015). Together, this supports the idea that future studies should aim for better representative samples.

Practical implications

The studies in the current thesis provided knowledge on how social learning skills manifest in different developmental stages. This informs what ages are most receptive to interventions for improving social skills such as social learning (Dahl et al., 2018; Yeager et al., 2018). Findings in this thesis show that social learning skills are rapidly improving from early and early-to-mid adolescence. These developmental phases would, therefore, be a key target window for monitoring social development, and for applying interventions that are targeted at stimulating well-adjusted social behavior in a typically developing population.

Furthermore, the insights from studies in typically-developing samples like in this thesis, are key for understanding developmental disorders (Karmiloff-Smith, 1998). Moreover, these findings provide important starting points for interventions for youth with maladaptive social tendencies and aberrant social decision-making, such as youth with conduct disorder problems or autism spectrum disorder (Frick & Viding, 2009; Hinterbuchinger et al., 2018; Izuma et al., 2011; Viding et al., 2012; Viding & McCrory, 2019).

Social deprivation during the COVID-19 pandemic

For a solid social development it is crucial to live in an enriched and stimulating living and learning environment, and social interactions with peers are one of the basic human needs (Baumeister & Leary, 1995). During the COVID-19 pandemic, globally the social environment was very limited due to measures such as social distancing and closure of schools and sport clubs. Although the measures of this pandemic had positive effects for some children (e.g., due to more time for parent-child bonding), most studies concluded negative effects on e.g., children's and adolescents' mood, emotional reactivity, and stress levels (Achterberg et al., 2021; Branje & Morris, 2021; Green et al., 2021). Moreover, although many youths showed to be resilient, increased numbers of adolescents with mental health problems were reported (Hollenstein et al., 2021). It should be noted that the findings described in the current thesis have been based on studies that have been conducted *before* the COVID-19 pandemic. Therefore, future studies are needed to assess whether this pandemic had long-term effects on adolescents' social development, or that they, for example, develop equally well but at a later age. Detrimental long-term effects may be limited because of the use of social media, which enabled people to have some sort of interactions and as such alleviate some of the adverse effects of physical distancing (Orben et al., 2020). However, a study using daily diaries in early adolescents during the pandemic showed that mood variability, related to experienced social attachment, was reduced for children who had offline contact with peers, whereas online contact did not influence mood variability (Asscheman et al., 2021). Especially longitudinal studies that started before, and will continue during and after the pandemic will be crucial for detecting long-lasting effects of the social constraints on social development.

Conclusion

In conclusion, in this thesis I aimed to investigate the development and underlying mechanisms of social learning in adolescence. The studies in this thesis show that adolescence is a key developmental period for developing well-adjusted social behaviors, and especially in the cooperative domain there are pronounced improvements. These studies make an important contribution to the literature on social development and learning, and may eventually contribute to interventions targeted at promoting well-adjusted behavior in typically developing adolescents, as well as youth with maladaptive social tendencies.

A

Addendum

Nederlande samenvatting
(Dutch summary)

References

List of publications

About the author

Dankwoord
(acknowledgements)

Nederlandse samenvatting

Als ik je zou vragen om drie dingen te noemen die je als kind of tiener hebt geleerd, welke zouden dat dan zijn? Waarschijnlijk denk je aan bepaalde vaardigheden of aan iets dat je uit schoolboeken hebt geleerd, zoals lezen, rekenen of fietsen. Dit zijn dingen die erg nuttig zijn om te leren, en die je vast al vaak hebt gebruikt. Naast het leren van zulke kennis of vaardigheden, bestaat er ook een ander soort leren: *sociaal leren*. Dat is het soort leren waarbij je *sociale* informatie leert. Je leert dan bijvoorbeeld over de mensen om je heen. Omdat mensen sociale wezens zijn, vormt sociale informatie het overgrote deel van wat we in ons leven leren. Dat wordt vooral duidelijk wanneer we in een hele nieuwe sociale omgeving komen, zoals na een verhuizing, bij een nieuwe baan, of op een nieuwe school. De meeste mensen ken je dan nog niet: wie zijn er aardig, en wie juist niet? Met wie zou je goed samen kunnen werken? Om daar achter te komen, moet je *sociaal leren*.

Er zijn verschillende vormen van sociaal leren. In mijn proefschrift heb ik me gericht op twee vormen: het leren *over* anderen, en het leren *voor* anderen. Bij het leren *over* anderen gaat het bijvoorbeeld om leren of je iemand kunt vertrouwen of niet. Het leren *voor* anderen wordt ook wel *prosociaal leren* genoemd (Lockwood et al., 2016). Hiermee wordt bedoeld dat je moet leren wat je het beste voor iemand kan doen om diegene te kunnen helpen. Bijvoorbeeld, om een verdrietige vriend te troosten, moet je weten hoe je diegene het beste kan opbeuren. Hoewel deze twee vormen van sociaal leren van elkaar verschillen, hebben ze ook overeenkomsten. Over het algemeen omvatten ze namelijk leren over wat we doen (onze acties) en de resultaten daarvan (uitkomst), waarbij andere mensen betrokken zijn.

Het goed kunnen leren in een sociale omgeving is een erg belangrijke sociale vaardigheid (Fareri et al., 2020). Daardoor weet je bijvoorbeeld met wie je kunt samenwerken (zoals in school- of bedrijfsprojecten), aan wie je je geheimen kunt toevertrouwen, en hoe je iemand het beste kunt helpen. Het kunnen leren over en voor anderen helpt je dus om keuzes, waarbij anderen betrokken zijn, goed te maken en om te bepalen hoe je je in de buurt van andere mensen het beste kan gedragen. Zulk adaptief (d.w.z, goed aangepast) gedrag is dus belangrijk om te ontwikkelen. Ook heeft eerder onderzoek laten zien dat goede sociale vaardigheden essentieel zijn voor je gezondheid en (emotioneel) welzijn op de lange termijn (Baumeister & Leary, 1995; House et al., 1988).

De adolescentie als belangrijke fase voor de ontwikkeling van sociale vaardigheden

Een periode in onze ontwikkeling waarvan wordt gedacht dat we deze complexe sociale leervaardigheden ontwikkelen, is de adolescentie. De adolescentie, grofweg tussen de 9 en 24 jaar oud, is namelijk een periode waarin ook veel andere sociale vaardigheden ontwikkelen en waarin er veel veranderingen plaatsvinden in de sociale omgeving. Zo brengen adolescenten bijvoorbeeld meer tijd door met hun vrienden dan met hun familie, en worden hun vriendschappen intenser en complexer (Brown & Larson, 2009; De Goede et al., 2009; Lam et al., 2014). Van de psychosociale veranderingen in de adolescentie wordt gedacht dat ze het gevolg zijn van de hersenontwikkelingen die plaatsvinden (Blakemore & Mills, 2014; Nelson et al., 2016; Sommerville, 2013). Door deze veranderingen in de sociale omgeving en in het brein, is het aannemelijk dat de adolescentie ook een belangrijke periode is voor het ontwikkelen van sociaal leren. Één hoofddoel van mijn proefschrift is om de ontwikkeling van sociaal leren in de adolescentie te onderzoeken.

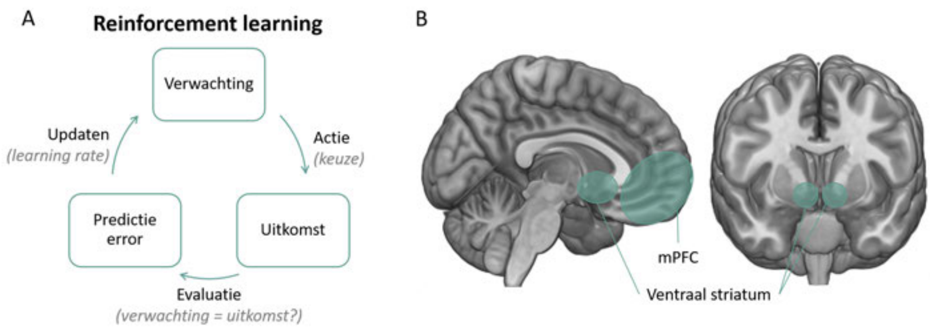
Computationele mechanismen van sociaal leren

Het ander hoofddoel van dit proefschrift is om de onderliggende mechanismen van sociaal leren in de adolescentie te onderzoeken. Zulke onderliggende mechanismen zijn factoren die leeftijdsverschillen en/of individuele verschillen in sociaal leren verklaren.

In mijn proefschrift heb ik onder andere gebruik gemaakt van het theoretisch kader *reinforcement learning* om de onderliggende mechanismen van sociaal leren in kaart te brengen (zie Figuur 1A). Reinforcement learning is het proces dat beschrijft hoe onze verwachtingen en eerdere ervaringen invloed hebben op onze toekomstige acties, en wordt met een wiskundige formule beschreven. Hierbij spelen ***predictie errors*** – het verschil tussen wat je verwacht en wat er daadwerkelijk gebeurt – een belangrijke rol. Als de uitkomst beter of slechter is dan verwacht, dan is er een predictie error. Hoe groter het verschil, hoe groter de predictie error. Deze predictie errors zorgen voor leren, omdat ze gebruikt worden voor het updaten van je verwachtingen met de nieuwe informatie. Zo zal een uitkomst dat beter is dan je verwacht (positieve predictie error) ervoor zorgen dat je in de toekomst vaker diezelfde actie zal verrichten. Terwijl je bij een uitkomst die slechter is dan je verwacht (negatieve predictie error) dat juist niet zo snel meer zal doen.

De mate waarin je je verwachtingen aanpast nadat er iets anders gebeurt dan verwacht (predictie error), wordt bepaald door je ***learning rate***. Als je een hoge learning rate heb, dan zal je drastisch je verwachtingen updaten in het geval van een predictie error. Met een lage learning rate, zullen je verwachtingen maar een beetje bijgesteld worden. Dat laatste kan gunstig zijn in situaties die vrij stabiel zijn, waardoor de informatie van een langere periode wordt gebruikt om verwachtingen te vormen.

Om wiskundige formules zoals die van reinforcement learning toe te passen op gedrag, gebruiken onderzoekers de methode *computationeel modelleren*. Computationeel modelleren houdt in dat wiskundige formules, zoals die van reinforcement learning, gebruikt worden om gedrag te beschrijven. Hierdoor is het mogelijk om factoren te identificeren die je niet direct aan het gedrag kunt zien of meten. Dit maakt computationeel modelleren een waardevolle methode om menselijk gedrag te onderzoeken. In mijn proefschrift heb ik computationeel modelleren toegepast op sociaal leren, om de onderliggende mechanismen van leeftijdsverschillen en/of individuele verschillen van sociaal leren in de adolescentie in kaart te brengen.



Figuur 1. (A) Reinforcement learning. De actie die je uitvoert, is gebaseerd op je verwachting van de uitkomst van die actie. Na je actie wordt er geëvalueerd of de daadwerkelijke uitkomst verschilt van de uitkomst die je had verwacht. Het verschil hiertussen wordt de predictie error genoemd. Als de werkelijke uitkomst afwijkt van je verwachting (predictie error ≠ 0), wordt dit gebruikt om je verwachtingen voor de volgende actie of keuze bij te werken. De mate waarin je je verwachtingen updatet, wordt bepaald door je *learning rate*. **(B)** Het ventraal striatum en de mediale prefrontale cortex (mPFC) zijn hersengebieden die betrokken zijn bij *reinforcement learning*.

Neurale mechanismen van sociaal leren

Een andere methode om onderliggende mechanismen van sociaal leren te onderzoeken, is *functionele neuroimaging*. Voor hersenonderzoek gebruiken wetenschappers vaak Magnetic Resonance Imaging (MRI) scanners. Dit is een niet-invasieve methode, dat ook geschikt is om bij kinderen en adolescenten toe te passen. Als de MRI scanner wordt gebruikt om hersenactiviteit te meten, wordt dit functionele MRI (fMRI) genoemd. Wanneer deelnemers een taak uitvoeren (bijvoorbeeld een sociale leertaak) tijdens het scannen, worden er om de paar seconden foto's van de hersenen gemaakt. Met deze techniek kunnen onderzoekers bestuderen welke hersengebieden bij welke onderdelen van de taken betrokken zijn.

Voor het onderzoeken van sociaal leren, is het nuttig om computationeel modelleren en fMRI te combineren. Zo kunnen de predictie errors uit de computationele modellen gebruikt worden in de fMRI analyses, zodat deze leersignalen in de hersenen kunnen worden bekeken. Belangrijke hersengebieden die betrokken zijn bij reinforcement learning, zijn het ventrale striatum en de mediale prefrontale cortex (mPFC) (zie Figuur 1B). Het striatum is een gebied in het midden van de hersenen, dat je gebruikt als je keuzes maakt, wanneer je iets leuk vindt, of als iets belonend is. Ook is het ventraal striatum belangrijk voor het berekenen van predictie errors. Het is daarom een belangrijk gebied voor (sociaal) leren (Olsson et al., 2020). Het striatum is verbonden met de mPFC, welke zich voor in het brein bevindt. Van de mPFC wordt gedacht dat het belangrijk is voor het nadenken over wat andere mensen denken, en om beslissingen te maken die te maken hebben met andere mensen. Daarnaast is de mPFC ook betrokken bij reinforcement learning (Joiner et al., 2017). Hoewel meerdere hersengebieden betrokken zullen zijn bij (sociaal) leren, wordt verwacht dat het ventraal striatum en de mPFC een sleutelrol spelen bij sociaal leren.

Dit proefschrift

Het doel van dit proefschrift is om de ontwikkeling en onderliggende mechanismen van sociaal leren in de adolescentie te onderzoeken. Ik focus me hierbij op (1) het leren *over* andere mensen, in het bijzonder of ze (on)coöperatief en (on)betrouwbaar zijn, en (2) het leren *voor* andere mensen, oftewel leren welke acties anderen kunnen helpen (prosociaal leren). Om de ontwikkeling van sociaal leren te onderzoeken, heb ik meerdere steekproeven onderzocht die de vroege tot late adolescentie beslaan (± 8-10 jaar tot ± 21-24 jaar). Om de onderliggende mechanismen te onderzoeken, die de leeftijdsverschillen en/of individuele verschillen in sociaal leren kunnen verklaren, heb ik gebruik gemaakt van zelfrapportage vragenlijsten, en van de methoden *computationeel modelleren* en *functionele neuroimaging* (fMRI).

Samenvatting van de resultaten

Leren over het gedrag van anderen in de adolescentie

In **hoofdstuk 2**, heb ik onderzocht hoe adolescenten leren *over* het gedrag van anderen. Aan dit onderzoek deden 244 jongeren tussen de 8 en 23 jaar mee. Deze jongeren hebben een aantal spellen met anonieme leeftijdsgenoten gespeeld. In die spellen konden ze leren welke tegenstanders zich overwegend coöperatief (betrouwbaar, samenwerkend), of overwegend niet-coöperatief (onbetrouwbaar, niet-samenwerkend) gedroegen. Door dat over de tegenstanders te leren en vervolgens hun eigen keuzes daaraan goed aan te passen, konden ze betere scores behalen in het spel. Zo was het in één van de spellen gunstig om de betrouwbare mensen te vertrouwen, terwijl ze de onbetrouwbare mensen beter niet konden vertrouwen. In een ander spel was het gunstig om een voordeel te accepteren van samenwerkende anderen, en om een nadeel te accepteren van niet-samenwerkende anderen.

We vonden dat de sociale leervaardigheden van adolescenten een asymmetrisch ontwikkelingspatroon lieten zien: al vanaf de vroege adolescentie (± 8-10 jaar) pasten de jongeren hun gedrag goed aan wanneer het gunstig was om niet-coöperatieve keuzes te maken (zoals iemand *niet* vertrouwen). Daarentegen we vonden een sterke verbetering in de vroeg-midden adolescentie (± 12-14 jaar) wanneer ze moesten leren dat het gunstig was om coöperatieve keuzes te maken (zoals iemand wél vertrouwen). Met gedragsanalyses en computationeel modelleren hebben we laten zien dat deze verbeteringen in sociaal leren deels verklaard konden worden door leeftijdsverschillen in 'aversie voor ongelijkheid'. Specifiek, vonden jongere adolescenten, vergeleken met de oudere adolescenten, het erger om minder te hebben dan iemand anders, wat er vervolgens voor zorgde dat ze hun gedrag minder goed aanpasten. Daarnaast vonden we met computationeel modelleren dat er ook leeftijdsverschillen in de *learning rates* (updaten van verwachtingen) waren. Terwijl de jongere adolescenten van begin tot het einde van het spel hun verwachtingen over de tegenstanders bleven updaten, hadden de oudere adolescenten (midden-adolescentie) halverwege het spel al stabielere verwachtingen. Daardoor waren deze oudere adolescenten beter in staat om meer informatie over de tegenstanders te gebruiken om tot een keuze te komen.

Tezamen suggereren de resultaten van dit hoofdstuk dat de vroeg-midden adolescentie een ontwikkelingsperiode is waarin er een snelle verbetering is in sociale leervaardigheden, en dat de verbeteringen vooral te zien zijn in het coöperatieve domein.

Flexibel leren over de betrouwbaarheid van anderen in de adolescentie

In **hoofdstuk 3**, heb ik voortgebouwd op het onderzoek in hoofdstuk 2. In deze studie gebruikte ik nogmaals het spel waarin de deelnemers konden leren over de betrouwbaarheid van anderen. Daar heb ik een onderdeel aan toegevoegd, waarin het gedrag van de tegenstanders – onaangekondigd - compleet veranderde van betrouwbaar naar onbetrouwbaar, en vice versa. Op die manier kon ik onderzoeken hoe flexibel adolescenten hun gedrag kunnen aanpassen nadat iemands betrouwbaarheid verandert. Ook was er een niet-sociaal onderdeel in het spel toegevoegd, waarin de deelnemers niet met andere jongeren speelden, maar met gokautomaten. Zo was het mogelijk om te onderzoeken of sociaal leren en niet-sociaal leren van elkaar verschillen. Aan dit onderzoek deden 157 adolescenten tussen de 10 en 24 jaar oud mee.

In lijn met de bevindingen van hoofdstuk 2, waren adolescenten van alle leeftijden er beter in om te leren wie ze *niet* konden vertrouwen dan wie ze wél konden vertrouwen. Voor beiden vonden we verbeteringen over leeftijd, al waren deze leeftijdsverbeteringen dit keer even sterk. Bij het onderdeel waarin de betrouwbaarheid van de tegenstanders plotseling omkeerde, vonden we wel weer een asymmetrie in de ontwikkelingspatronen: alle leeftijden pasten even snel hun gedrag aan wanneer de tegenstander onbetrouwbaar was geworden. Maar om te leren dat een onbetrouwbaar iemand opeens toch wel betrouwbaar was geworden, leerden de oudere adolescenten beter dan de jongere adolescenten. Deze flexibiliteit was het sterkst vanaf de midden-adolescentie, en was dus ook in dit onderzoek het sterkst in het coöperatieve domein (leren wél te vertrouwen). We vonden geen verschillen tussen sociaal en niet-sociaal leren, want lijkt te suggereren dat er een sterke overlap is tussen deze twee vormen van leren, of dat verschillende onderliggende mechanismen tot hetzelfde gedrag hebben geleid (Morton, 2010).

Daarnaast heb ik in deze studie ook onderzocht of iemands opvoeding invloed heeft op sociale leervaardigheden. Hoewel de adolescentie een periode is waarin leeftijdsgenoten een belangrijke rol spelen, kunnen onze kijk op de wereld en onze verwachtingen over anderen ook worden beïnvloed door onze thuisomgeving. Eerder onderzoek heeft bijvoorbeeld aangetoond dat personen die opgroeien in huishoudens met overwegend negatieve opvoedingsstijlen (zoals het uiten van negatieve emoties), en fysieke en emotionele verwaarlozing, een verhoogde kans hebben op verminderd sociaal functioneren (Gobin & Freyd, 2014; McCrory & Viding, 2015; Overbeek et al., 2020). Het was echter nog niet bekend of omgevingsfactoren zoals de opvoeding ook van invloed zijn op de sociale leervaardigheden van adolescenten. In dit onderzoek heb ik aangetoond dat adolescenten die aangaven meer negatieve opvoedingspraktijken te hebben ervaren (met name slechtere ouderlijke controle) minder flexibel waren in hun sociaal leren. In het bijzonder uitten ze te veel vertrouwen naar tegenstanders die plotseling onbetrouwbaar waren geworden.

Concluderend, wijzen deze resultaten op de adolescentie als een periode waarin sociale leervaardigheden adaptiever worden, en vanaf de midden-adolescentie ook steeds flexibeler worden. Echter kan het sociale leervermogen beïnvloed worden door iemands gezinsomgeving.

Effecten van verwachtingen op vertrouwensgedrag

In **hoofdstuk 4** heb ik de keuzes van adolescenten om te vertrouwen, en de onderliggende cognitieve mechanismen, verder onderzocht. Wanneer we besluiten om iemand te vertrouwen, is er onzekerheid of ons vertrouwen wordt beschaamd. Deze onzekerheid kun je vaak verminderen door informatie te verzamelen over de ander, bijvoorbeeld over hoe betrouwbaar diegene in het verleden is geweest. Het vermogen om onze verwachtingen over de betrouwbaarheid van anderen te updaten met de nieuwe verzamelde informatie, is een essentieel onderdeel van adaptief sociaal gedrag. In dit onderzoek (*N* = 157, 10-24 jaar, dezelfde steekproef als in hoofdstuk 3) heb ik onderzocht hoe en hoeveel informatie adolescenten verzamelen over de betrouwbaarheid van anderen om te beslissen of ze hen al dan niet vertrouwen. Daarnaast heb ik onderzocht hoe ze deze informatie gebruiken om hun verwachtingen over de betrouwbaarheid van deze anderen te updaten.

In lijn met de bevindingen uit hoofdstuk 2 en 3 lieten de gedragsanalyses zien dat oudere adolescenten, vergeleken met jongere adolescenten, adaptiever gedrag lieten zien. Zo vertrouwden ze in vergelijking met de jongere adolescenten vaker als de anderen betrouwbaar waren, en verzamelden ze vooral meer informatie wanneer de informatie uit hun steekproef nogal inconsistent was (zoals 50% van de keren betrouwbaar) dan wanneer hun steekproef consistent was (zoals 100% van de keren betrouwbaar). Met behulp van computationeel modelleren hebben we de onderliggende processen hiervan kunnen onderzoeken. Dit liet zien dat de grootste leeftijdsverschillen zaten in de *onzekerheid over hun verwachtingen*, wat aangeeft hoeveel variatie in betrouwbaarheid ze verwachten tegen te komen. In de vroeg-midden adolescentie nam deze onzekerheid het sterkst toe. Deze toegenomen onzekerheid bij de oudere adolescenten leidde ertoe dat niet zozeer hun verwachtingen maar de verzamelde informatie bepaalde of ze iemand zouden vertrouwen of niet.

Deze bevindingen wijzen dus op de vroege tot midden adolescentie als een ontwikkelingsfase waarin adolescenten meer openstaan voor mogelijke individuele verschillen in de betrouwbaarheid, waardoor ze flexibel kunnen leren dat sommige mensen betrouwbaar zijn en andere niet.

Prosociaal leren in de adolescentie

In hoofdstuk 5 heb ik een andere vorm van sociaal leren onderzocht: prosociaal leren. In deze fMRI studie heb ik de ontwikkeling en onderliggende computationele en neurale mechanismen van prosociaal leren onderzocht in 74 adolescenten tussen de 9 en 21 jaar oud. In een prosociale leertaak kregen de deelnemers telkens de keuze tussen 2 plaatjes. Het ene plaatje was vaak gekoppeld aan een beloning, terwijl het andere plaatje vaak was gekoppeld aan verlies. Na een aantal rondes konden de deelnemers leren met welk plaatje ze de meeste beloningen konden verdienen. Soms speelden ze dit voor zichzelf, en dan was de beloning voor zichzelf. Soms speelden ze voor iemand anders – een onbekende andere deelnemer in het onderzoek – wat prosociaal leren beoogde te meten.

De gedragsanalyses lieten zien dat adolescenten tussen 9 en 21 jaar in staat zijn om te leren om beloningen te verkrijgen voor zichzelf en voor anderen. De oudere adolescenten konden, vergeleken met jongere adolescenten, beter leren voor zowel zichzelf als voor een ander. Echter was het vooral het prosociaal leren dat de sterkste verbetering liet zien over leeftijd. Door middel van computationeel modelleren konden we de learning rates en predictie errors voor prosociaal leren onderzoeken. Ook de learning rates lieten de sterkste verbetering zien wanneer het ging om prosociaal leren versus leren voor zichzelf. De predictie errors hebben we toegepast in de fMRI analyses, zodat we deze leersignalen in het brein konden onderzoeken. De predictie errors voor het leren voor jezelf vonden we terug in het ventraal striatum. Deze leersignalen lieten geen leeftijdsverschillen zien. Daarentegen waren de predictie errors voor prosociaal leren gerelateerd aan activiteit in de ventromediale prefrontale cortex. Deze predictie error activatie tijdens prosociaal leren nam toe over leeftijd, en was daarnaast ook gerelateerd aan individuele verschillen in empathie.

Deze resultaten tonen aan dat ook prosociaal leren verbetert in de vroeg-midden adolescentie, zowel op gedrags-, computationeel-, en neuraal niveau. In lijn met de vorige hoofdstukken laat ook dit hoofdstuk zien dat leeftijdsverschillen het sterkst zijn voor gedrag dat met andere mensen te maken heeft.

Discussie en implicaties

Adolescentie als een belangrijke ontwikkelingsperiode voor het ontwikkelen van adaptief sociaal gedrag

In de empirische hoofdstukken van dit proefschrift heb ik onderzocht hoe leren over en leren voor anderen ontwikkelt in de adolescentie. Deze leeftijdsverschillen heb ik bestudeerd in steekproeven met een brede leeftijdsrange, van de vroege adolescentie (± 8-10 jaar) tot de late adolescentie (± 21-24 jaar). In dit proefschrift heb ik met verschillende studies laten zien dat de vroeg-midden adolescentie een periode is waarin de sociale leervaardigheden verbeteren. Zulke verbeteringen, zeker in het sociale domein, zijn met name relevant in een ontwikkelingsfase zoals de adolescentie. In de adolescentie zijn er namelijk veel veranderingen in sociale relaties, zoals het opbouwen van hechte vriendschappen. Daarnaast komen adolescenten steeds meer in aanraking met sociale situaties op school, sportclubs, en andere sociale gelegenheden (Fuligni, 2009). Adolescenten hebben dus belang bij het vertonen van adaptief sociaal gedrag, waar goede sociale leervaardigheden voor nodig zijn.

Daarnaast heb ik in dit proefschrift laten zien dat de verbeteringen van sociaal gedrag over leeftijd vooral, of het sterkst, plaatsvinden in het *coöperatieve* domein (zoals leren wél te vertrouwen, en prosociaal leren). Dit is in lijn met eerder onderzoek dat aantoont dat gedrag dat op anderen gericht is ('other-oriented behavior') – zoals coöperatief gedrag – verbetert in de adolescentie (Crone & Fuligni, 2020). Er wordt gesuggereerd dat de adolescentie een belangrijke periode is voor het creëren van de juiste balans tussen de behoeften van jezelf en die van anderen. Door die balans ben je in staat om goede sociale banden met anderen te vormen, en om een goede bijdrage te leveren aan de maatschappij (Crone & Fuligni, 2020; Fuligni, 2019). Dit kwam bijvoorbeeld ook terug in hoofdstuk 2 waarin oudere adolescenten het minder erg vonden om wat minder te hebben dan iemand anders, wat vervolgens bevorderlijk was voor het goed aanpassen van hun gedrag aan anderen. Samengevat zijn de bevindingen van dit proefschrift in lijn met de hypothese dat we naarmate we ouder worden minder 'egoïstisch' worden, en dat we beter in staat zijn om met anderen te werken aan collectief welzijn, ook al is dit niet altijd even gunstig voor onszelf als voor een ander.

Hoewel de resultaten van dit proefschrift inzicht geven in de ontwikkelingspatronen van sociaal leren, moet er wel worden opgemerkt dat de resultaten gebaseerd zijn op cross-sectionele studies. Dat houdt in dat elke proefpersoon slechts op één tijdspunt is onderzocht. Om ontwikkelingspatronen goed in kaart te brengen, zijn longitudinale studies echter geschikter. Met longitudinale studies worden proefpersonen op meerdere momenten onderzocht, en kan bijvoorbeeld onderzocht worden of en hoe sterk iemands sociale leervaardigheden verbeteren door de jaren heen. Longitudinaal vervolgonderzoek is dus nodig om de gevonden ontwikkelingspatronen in sociaal leren te bevestigen.

Het toepassen van computationeel modelleren om de ontwikkeling van sociaal gedrag te onderzoeken

In dit proefschrift heb ik computationeel modelleren toegepast om de ontwikkeling van sociaal leren te onderzoeken. Dat is een vrij innovatieve benadering geweest: pas sinds een aantal jaar worden computationele modellen toegepast op niet-sociaal leren in kinderen en adolescenten (Nussenbaum & Hartley, 2019). Het toepassen van computationele modellen op *sociaal* leren is voornamelijk gedaan bij data van volwassen proefpersonen (Joiner et al., 2017; Lockwood et al., 2020; Olsson et al., 2020). De computationele mechanismen van sociaal leren in de adolescentie zijn dus nog nauwelijks onderzocht.

De computationele modellen in dit proefschrift hebben tot meerdere inzichten geleid. Zo heb ik bijvoorbeeld laten zien dat learning rates voor het leren *over* anderen (hoofdstuk 2) en het leren *voor* anderen (hoofdstuk 5) afnamen over leeftijd. Deze afnames in learning rates waren gerelateerd aan verbeteringen in sociale leervaardigheden. De sociale leeromgevingen in dit proefschrift waren echter vrij stabiel; toekomstig onderzoek moet aantonen of zulke patronen er ook zijn in veranderende of onvoorspelbare sociale omgevingen. Ten tweede, hebben de computationele modellen in hoofdstuk 4 inzicht gegeven in onderliggende cognitieve mechanismen van sociaal gedrag. Computationeel modelleren heeft een voordeel ten opzichte van het gebruik van vragenlijsten, aangezien die laatste bijvoorbeeld kunnen leiden tot sociaal-wenselijke antwoorden (Althubaiti, 2016). Tot slot, hebben de computationele modellen ervoor gezorgd dat de leersignalen (predictie errors) in het brein onderzocht konden worden. Dit is een nauwkeurigere methode dan slechts het bekijken van neurale activatie tijdens positieve en negatieve uitkomsten, en geeft nieuwe inzichten in menselijk sociaal gedrag (zie Lockwood & Klein-Flügge (2020) voor een overzicht). Daarom raad ik aan dat toekomstig ontwikkelingsonderzoek naar (sociaal) leren ook streeft naar het gebruik van computationele leerparameters in de fMRI analyses.

Praktische implicaties

De studies in dit proefschrift hebben kennis opgeleverd over hoe sociale leervaardigheden zich manifesteren in de adolescentie. Deze inzichten in de ontwikkeling geven aan welke leeftijden het meest ontvankelijk zijn voor interventies voor het verbeteren van sociale vaardigheden, zoals sociaal leren (Dahl et al., 2018; Yeager et al., 2018). De bevindingen in dit proefschrift hebben aangetoond dat de vroeg-midden adolescentie de sterkste ontwikkeling van sociale leervaardigheden laat zien. Dat maakt deze periode erg geschikt voor interventies die erop gericht zijn om sociale vaardigheden, waaronder sociaal leren, te verbeteren in typisch ontwikkelende jongeren.

Verder zijn de inzichten uit studies in typisch ontwikkelende jongeren zoals in dit proefschrift essentieel voor het begrijpen van ontwikkelingsstoornissen (Karmiloff-Smith, 1998).

Bovendien bieden deze bevindingen belangrijke aanknopingspunten voor interventies voor jongeren met afwijkend sociaal gedrag, zoals jongeren met antisociale gedragsstoornissen of autismespectrumstoornis (Frick & Viding, 2009; Hinterbuchinger et al., 2018; Izuma et al. al., 2011; Viding et al., 2012; Viding & McCrory, 2019).

Gemis aan sociale interacties tijdens de COVID-19 pandemie

Voor een degelijke sociale ontwikkeling is het cruciaal om in een verrijkte leef- en leeromgeving te leven, met voldoende sociale interacties met leeftijdsgenoten (Baumeister & Leary, 1995). Tijdens de COVID-19-pandemie was de sociale omgeving voor mensen over de hele wereld zeer beperkt, door maatregelen als *social distancing* en het sluiten van scholen en sportclubs. Hoewel de maatregelen van deze pandemie voor sommige jongeren positieve effecten hadden (bijvoorbeeld doordat ouders meer tijd met hun kinderen konden doorbrengen), concludeerden de meeste onderzoeken negatieve effecten op bijvoorbeeld de stemming, emotionele reactiviteit en stressniveaus van kinderen en adolescenten (Achterberg et al., 2021; Branje & Morris, 2021; Green et al., 2021). Bovendien, hoewel veel jongeren veerkrachtig bleken te zijn, werden er meer adolescenten met psychische problemen gerapporteerd (Hollenstein et al., 2021).

De bevindingen die in dit proefschrift worden beschreven, zijn gebaseerd op onderzoeken die zijn uitgevoerd vóór de COVID-19-pandemie. Toekomstig onderzoek is dus nodig om te beoordelen of deze pandemie langetermijneffecten heeft op de sociale ontwikkeling van adolescenten, of dat ze zich bijvoorbeeld even goed ontwikkelen, maar wellicht op latere leeftijd. Vooral longitudinaal onderzoek dat voor de pandemie is gestart, en tijdens en na de pandemie zal worden voortgezet, zal cruciaal zijn voor het detecteren van langdurige effecten van de sociale beperkingen in deze pandemie op de sociale ontwikkeling.

Conclusie

Concluderend, heb ik in dit proefschrift de ontwikkeling en onderliggende mechanismen van sociaal leren in de adolescentie onderzocht. De studies in dit proefschrift laten zien dat de adolescentie een belangrijke periode is voor het ontwikkelen van adaptief sociaal gedrag, en vooral in het coöperatieve domein zijn er duidelijke verbeteringen. Deze studies leveren een belangrijke bijdrage aan de wetenschappelijke kennis over de sociale ontwikkeling en leren. Daarnaast kunnen de bevindingen bijdragen aan interventies die gericht zijn op het bevorderen van adaptief gedrag bij typisch ontwikkelende adolescenten, evenals jongeren met antisociale neigingen.

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About the author

Bianca Westhoff was born on August 17th, 1992 in Amsterdam, The Netherlands. After graduating from secondary school (gymnasium, Montessori Lyceum Amsterdam) in 2010, she obtained her bachelor's degree in Psychobiology in 2013 from the University of Amsterdam. During her master's, she spent an extra semester abroad at The University of British Columbia in Vancouver, Canada. She obtained her Research Master Psychology degree (major in Brain & Cognition, minor in Psychological Methods) at the University of Amsterdam in 2016. During her master's, Bianca did an internship at the Brain and Development Research in Leiden, where she was involved in the longitudinal Braintime study. Concurrently, she wrote her master thesis on developmental changes in resting-state functional connectivity across adolescence, under supervision of dr. Anna van Duijvenvoorde.

In November 2016, Bianca started her PhD project at Leiden University under supervision of dr. Anna van Duijvenvoorde and prof. dr. Eveline Crone. In the interdisciplinary project *Samen Leren* (Learning Together) she examined the development and (neural) mechanisms of social learning in typically developing adolescents. In addition to her research and teaching activities, Bianca was a board member of the PhD Platform which advises the Faculty of Social Sciences on various PhD-related matters, such as the supervision and mental wellbeing of PhDs.

After completing her PhD research in September 2021, Bianca continued working as a teacher at Leiden University. As of February 2022, she started working as a researcher at VeiligheidNL.

Dankwoord

Eindelijk is het zover: m'n proefschrift is AF! Wat een rollercoaster was dat, en wat heb ik veel geleerd. Over adolescenten, over hun (sociale) leervaardigheden en hersenen, over onderzoek doen, over de academische wereld… Maar vooral heb ik veel over mezelf geleerd, en hoe belangrijk en fijn het is om leuke, lieve, gezellige, en *supportive* mensen om je heen te hebben. En dat zijn er de afgelopen jaren heel wat geweest! Ik hoop dat jullie stuk voor stuk beseffen dat ik jullie enorm heb gewaardeerd (en nog steeds doe!), en dat dit proefschrift er zonder jullie niet was geweest.

Allereerst wil ik natuurlijk mijn co-promotor Anna bedanken dat ze het Samen Leren avontuur met mij durfde aan te gaan. Wat hebben we veel meegemaakt. Onze reizen gingen niet altijd even soepel (e.g., de treinreis uit Berlijn), maar uiteindelijk bereikten we altijd de bestemming! Bedankt voor al je enthousiasme, geduld, en steun, maar ook voor de gezellige bijklets-momenten. En hoe bijzonder dat de geboortes van jouw 3 fantastische kids de grootste en belangrijke momenten van mijn PhD markeren! Ik ben je heel dankbaar voor alle kansen die je me hebt gegeven, en wat je me hebt geleerd, als onderzoeker en als mens. Dan mijn promotor Eveline. Ja, nu ben ik wél de volgende die aan de beurt is om te promoveren ;). Bedankt voor al je enthousiasme, en je motiverende berichtjes die je altijd wist te timen op de momenten dat ik ze het best kon gebruiken. De oppeppers en de plan-van-aanpak meetings hebben me zeker over de laatste hobbels geholpen. Ik weet zeker dat we elkaar nog tegen blijven komen (misschien eindelijk eens bij een nieuwjaarsduik?), en ik blijf zeker volgen hoe gepassioneerd je je inzet om de wereld van jongeren beter te begrijpen én te verbeteren.

A

Dear Wouter, Lucas and Essi, dear ORA team: thank you for this exciting collaboration. I enjoyed our meetings in Leiden, Berlin, London, and Amsterdam, and I have learned a lot from all of you. Thank you for all your valuable input and efforts to our Leiden-based ORA projects.

Natuurlijk wil ik ook mijn fantastische paranimfen bedanken. Neeltje, niemand begreep mijn struggles beter dan jij, en je wist me altijd weer moed in te spreken. En niemand kan enthousiaster successen en mijlpalen meevieren dan jij. Een terechte "über-paranimf" dus, en ik ben heel blij dat je als paranimf dit avontuur met mij wil afsluiten! Susanne, met jou in de buurt is het altijd een feestje. Inmiddels kennen we elkaar alweer bijna 12(!) jaar, en zijn we zelfs voor de 2^{e} keer collega's! Dankjewel voor alle fijne gesprekken over van alles en nog wat, de gezelligheid, en voor je steun op ook dit bijzondere moment.

Dan mijn lieve mede-AIOs, die mijn PhD van dichtbij hebben meegemaakt. Laura, bedankt voor alle kletspraatjes en mental support zowel op/over werk als privé. Renske, dankzij jou heb ik de racefiets ontdekt! Hopelijk blijven we samen mooi-weer rondjes fietsen, ookal woon je inmiddels aan de andere kant van het land. Jochem, bedankt voor alle keren dat je te hulp schoot (e.g., bij scanchoas, en e-prime errors), voor je humor en voor alle herkenbare gesprekken - we zijn goed genoeg! Suzanne, bedankt voor alle 'eerste keren' als stagiair en als PhD (dataverzameling, congres, onderwijs geven, etc.) die we samen meemaakten en waarover we konden sparren. Ilse, mijn fijne kamergenootje, die altijd klaar stond om te helpen uitvinden waarom R nu weer zo stom deed. Dankjewel voor de goede gesprekken, en dat je mij leerde hoe je nou écht goede en mooie posters maakt. Bedankt Mixed-Brainers Iris, Jorien, Christel, dankzij jullie was het afschrijven van mijn proefschrift tijdens een pandemie een stuk minder eenzaam. En natuurlijk ook nog alle andere collega's en (oud)labgenootjes (Andrik, Anna vS, Annelinde, Berna, Eduard, Emmy, Fabienne, Ili, Isabel, Jiska, Kiki, Lara, Lisa, Lina, Mara, Marieke, Marjolein, Michelle, Neeltje vdB, Philip, Sabine, Sanne, Sarah, Sibel, Simone B, Simone D, Zdena, en alle anderen), bedankt voor de gezelligheid en de leuke (wetenschappelijke) discussies en gesprekken! Marloes, Amy, en Friederike, mijn mede-bestuursgenoten van het PhD Platform. Ik vond het heel tof om onderdeel van het Platform te zijn, maar het was vooral super om dit met jullie te mogen doen!

Uiteraard bedank ik ook alle scholen, jongeren, en hun ouders die mee hebben gedaan aan mijn projecten. Daarnaast wil ik ook alle studenten en onderzoeksassistenten (in het bijzonder: Sander, Myrna, Ellina, Sophie, Roos, Caroline, en Cevdet) heel erg bedanken voor al jullie inspanningen en enthousiasme bij de dataverzamelingen. Zonder jullie had ik deze fantastische datasets op de scholen en bij de scanner nooit kunnen verzamelen. Ik vond het een feestje om met jullie te werken, en heb genoten van de waanzinnige team spirit. LIBC-support, bedankt voor jullie hulp bij de fMRI studies, en dat jullie 24/7 paraat stonden voor urgente vragen.

Lieve vrienden, dankjewel voor jullie support, en de nodige afleiding en ontspanning tijdens de gezellige etentjes, borrels, wandelingen, fietstochtjes, escaperooms, en spelletjesavonden.

Lieve papa, mama, Lisa, familie, en schoonfamilie. Waarschijnlijk weten jullie nog steeds niet precies wat ik de afgelopen jaren nou eigenlijk heb gedaan, maar jullie steun en aanmoedigingen waren er zeker niet minder om. Bedankt voor alles!

Lieve Floor, wát zal jij blij zijn dat dit proefschrift nu eindelijk klaar is ;-). Dankjewel voor je steun en geduld, voor je knuffels bij de tegenslagen, en voor het meevieren van de mijlpalen. Ik hou van je, en ik kijk uit naar alle avonturen die we nog samen gaan beleven!