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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.