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Moral learning and decision-making across the lifespan

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Abstract

Moral learning and decision-making are crucial throughout our lives from infancy to old age. Emerging evidence suggests that there are important differences in how we learn and decide in moral situations, and these may be underpinned by co-occurring changes in the use of model-based values and theory of mind. Here, we review the decision neuroscience literature on moral choices and moral learning considering four key concepts. These concepts are learning and experiencing moral emotions, learning and deciding about other's moral character, moral learning and deciding for others, and moral influence and contagion. We focus on recent behavioural and neuroimaging findings using a value-based decision-making framework, showing how mathematical models of decision-making can be used to determine the computational mechanisms underlying these concepts, uncover their neural correlates, and ultimately provide a mechanistic account of morality across the whole lifespan.

Keywords: Moral, decision-making, lifespan, computational, learning, brain

Introduction

The question of what makes humans moral has been of interest to philosophers, psychologists, economists, and sociologists for centuries. At a basic level, we can define morality as the set of norms and values subscribed to by a social group to guide its actions in terms of good and bad (Crockett 2013; DeScioli & Kurzban 2009; Qu et al. 2022; Tomasello & Vaish 2013). A key question is how and when such morality develops, and does it differ across our lifespan? In addition, research has begun to focus on using mathematical computational models of value-based learning and decision-making to link cognition, behaviour and neural activity (Crockett 2013; Qu et al. 2022). How can we use this framework to understand the development of learning and decision-making in a moral context, and are some of the foundational components of these models apparent from infancy to old age?

Some have argued that infants are born with an innate moral sense (Bloom & Wynn 2016; Hamlin 2013; Wynn et al. 2018) whereas others emphasise the role of the social environment more strongly in the acquisition of morality (Dahl & Paulus 2019). However, the extent to which we are moral is multifaceted and may indeed differ across our whole lifespan from infancy to older age (Cutler et al. 2021a; Mayr & Freund 2020). Here we argue that to understand the unique interaction of development on morality it may be crucial to take such a lifespan perspective and to do so within a value-based framework of reinforcement learning (**Figure 1, RL sidebar**). In parallel, the basic mechanisms of moral learning and decision-making likely depend on cognitive processes that also differ with age, such as model-based learning and theory of mind (**Figure 2**). Understanding how these related processes develop and change can bring us insights into the dynamic fluctuations of basic building blocks of morality across our lives.

We suggest that four key components underlie morality from infancy to older adulthood. There are likely other processes important for moral learning and decision-making. Yet, these four components provide a framework to draw parallels across age. The first component is learning and experiencing moral emotions. How do we learn and experience emotions such as guilt, envy and empathy? The second concept is learning and deciding about other's moral character. How do we learn moral norms, and how do we decide whether others have abided by them? The third concept is moral learning and deciding for others. How do we learn to be prosocial and make decisions that help and avoid harming other people, and how do we punish other people when they violate norms? Finally, how do others' moral norms influence ourselves, through moral influence and contagion. We consider each of these concepts in turn to provide a taxonomy of moral decision-making that can be relevant throughout our lives.

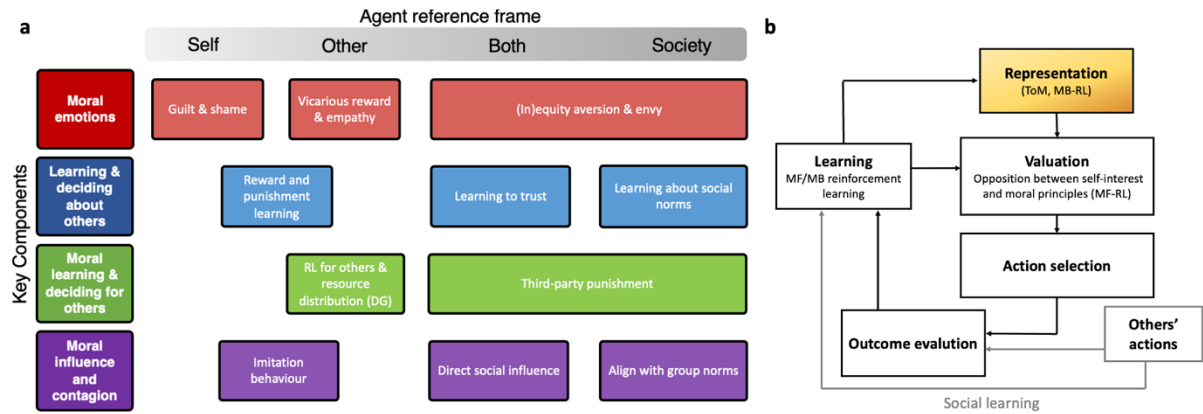


Figure 1. Lifespan framework for moral learning and decision-making. (a) We propose four key components underlie morality from infancy to older adulthood. These components provide a framework to draw parallels across ages that can provide new insights into the fundamental nature of morality. We suggest that outside of these four components, we should also consider the agent reference frame, i.e. whether moral choices are about or for self, other, both, or society. (b) A conceptual framework describing the computations involved in moral decision-making that can be separated into distinct components. The first consists of the representations of the moral dilemma that encompass the moral principles or norms involved as well as the mental states and intentions of others (Theory of Mind: ToM). Then, individuals evaluate each possible action by weighing the personal benefit against the consequences for others. Third, individuals select the action that maximizes their utility following moral principles and moral norms. Fourth, they evaluate the outcome based on the consequences of their moral action and based on other's reactions to it, these outcomes are often experienced as moral emotions. Finally, a learning signal is used to update individuals' model of the world (Model-based reinforcement learning: MB-RL), and the expected value of specific actions (Model-free reinforcement learning: MF-RL). Note that learning from the consequences of others' actions is ubiquitous and can lead to updates of our world model and the direct expectation of outcomes of actions. Abbreviations: DG, Dictator Game, RL, reinforcement learning

Learning and experiencing moral emotions

Moral emotions are those emotions that underpin our capacity for morality (Tangney et al. 2007). These may include guilt, envy and empathy. The onset of moral emotions coincides with the development of the ability to distinguish self from others (**Figures 1b & 2**). These emotions can further be grouped as positive (e.g., pride) or negative (e.g., guilt, envy) (Bastin et al. 2016). One common characteristic of negative moral emotions is that they occur when individuals break social norms, which are internalized as values. Moral emotions may serve to regulate moral behaviour, helping individuals to follow social norms. The development of moral emotions such as envy allows us to experience disadvantageous inequity aversion, where we disfavour unfair allocations of value. How and when these processes develop and differ across the lifespan is therefore essential to understand. In the following sections, we consider the development of moral emotions from infancy to old age.

Moral emotions in infancy and childhood

From our first days, we rapidly develop abilities in visual, motor and auditory domains (Tierney & Nelson 2009). This is well-established. However, our propensity for moral emotions is much less well understood. Some have argued that infants are born with a sense of morality that provides a foundation for the rest of life (Bloom & Wynn 2016; Hamlin 2013; Wynn et al. 2018). Given the challenges with reliably measuring infant emotions and behaviour, several studies have sought to understand if infants experience moral emotions through observational studies. Here we focus on moral emotions including guilt, fairness and empathy which have been examined the most extensively in this age group.

The literature on when guilt emerges is somewhat mixed. One seminal study suggested that 8-year-olds were more likely to experience guilt than 4-year-olds. And this effect was replicated in various studies around the world (Krettenauer et al. 2008). Other studies have suggested that guilt and shame may develop early in life in toddlers. For example, in the broken toy paradigm (Cole et al. 1992) a child believes they have broken an adult's favourite toy. Infants display more guilt and shame (as rated by observers) to this event than in contexts where they simply engage in free play (Cole et al. 1992).

In parallel, the transition from infancy to childhood is associated with development in the complexity of our understanding of inequity. Inequity aversion is where people consider their own material self-interest but also the resources of others (Fershtman et al. 2012). Children aged 4 show disadvantageous inequity aversion to unequal divisions of resources (Blake & McAuliffe 2011; Fehr et al. 2008; McAuliffe et al. 2013; Sheskin et al. 2014). Researchers have also examined childhood facial expressions in response to unfairness at receiving less than a peer. In this context, 3 to 5-year-olds respond with negative emotional expressions when receiving less but neutral to positive expressions when they receive more (House et al. 2012; LoBue et al. 2011).

As we transition from infancy to childhood a sense of self and other distinction emerges that supports the development of empathy, the capacity to vicariously experience the affect and cognition of other people, beyond simply experiencing emotional contagion (Decety & Holvoet 2021; Frick & Kemp 2021; Lockwood 2016). Indeed, theoretical accounts suggest that when emotional contagion is experienced with self-other distinction it may be conceptualised as empathy (Decety & Meyer 2008; Lockwood 2016). These cognitive and affective changes are likely underpinned by structural and functional brain maturation (Decety & Michalska 2010; Mills & Tamnes 2020). In turn, such developmental processes support more complex value-based and decision-making architecture. For example, recent work suggests that children aged 5-6 can infer the cost-benefit utility of others' competencies and preferences (Jara-Ettinger et al. 2016).

Finally, children increase their understanding of intentional vs. unintentional harm to guide behaviour (Amsterdam 1972; Steinbeis 2016). When the self rather than another person is the source of harm or help, 4- to 6-year-olds can attribute negative emotions to transgressors who violate social norms unintentionally (Nunner-Winkler & Sodian 1988). This contrasts with before this age where there is little distinction between intentional and unintentional harm (Nunner-Winkler & Sodian 1988). With developing architecture of moral emotions including self-other distinction, understanding intentional vs unintentional harm, inference regarding costs and benefits, and co-occurring brain maturation, this sets the scene for further complexity of moral emotions in the transition to adolescence.

Moral emotions in adolescence

As children transition to adolescence, they increase their self-awareness and become more preoccupied with their peers. Subsequently, they may feel moral emotions like guilt and shame more often and more deeply (Zeman et al. 2006). In adolescence, moral emotions of guilt and fairness have been frequently studied with economic games, specifically the Dictator, Trust, and Ultimatum Games (DG, UG, TG) (Fett et al. 2014; Güroğlu et al. 2014; Güroğlu et al. 2009; van den Bos et al. 2010). According to the Fehr-Schmidt inequity aversion model, two parameters govern the utility of resources that are split by two parties (Fehr & Schmidt 1999). This first one is guilt, expressed as the utility attributed to giving up on one own pay-off to achieve a more equal outcome. The second is envy, which expresses how one dislikes unequal outcomes in the advantage of the other leading to disadvantageous inequity aversion described above.

In the DG, participants are asked to divide money or points between him or herself and another player. In this game any non-zero offerings are examples of guilt. Recent evidence shows that, in context of different variations of the DGs, social contextual factors such as the target of giving increasingly

influence adolescent decision-making. For example, Guroglu et al., 2014 showed that with increasing age adolescents start to differentiate their sharing behavior between different types of peers in their classroom. Later studies also showed that the extent to which adolescents differentiate between others depends on their level of perspective-taking (van de Groep et al. 2020). Moreover, a recent study showed that donations to charity increased across adolescence, indicating an increasing interest in societal goals (Spaans et al. 2023). Finally, self-report studies have shown adolescents prone to experiencing guilt were more likely to show higher levels of prosocial behaviour and lower levels of aggression (Roos et al. 2013; Stuewig & McCloskey 2005; Zeman et al. 2006). Taken together these results suggest a shift from a model-free (outcome-based) towards a model-based (rule/norm-based) decision-strategy, in which adolescents take the perspective of others, and society increasingly into account.

A similar developmental pattern is seen in context of the UG, specifically, the mini-UG. Here the proposer only has two options, an unfair and an alternative offer. The alternative is either an equal split or another unfair offer. When the first player proposed an unfair offer (8/2) when the alternative was fair (5/5), players of all ages rejected unfair offers. But when the first player had no alternative (8/2 vs. 8/2), the number of times participants accepted an unfair offer increased with age, indicating an increase in taking intentions into account (Gummerum & Chu 2014; Güroğlu et al. 2009). A developmental neuroimaging study further revealed an age-related increase inactivation in the dorsolateral prefrontal cortex (dlPFC) and Temporo-Parietal Junction (TPJ), which correlated with the increased sensitivity to others intentions (Güroğlu et al. 2011). In sum, these results highlight that self-regulation (dlPFC) and perspective taking (TPJ) become more important processes in adolescent moral decision-making.

Finally, empathy involves both feeling others pain and sharing their joy (Lockwood 2016). The response to vicarious rewards, rewards received by others, provides a fundamental insight into the value placed on the welfare of others, is considered a necessary foundation for empathizing (Bird & Viding 2014), and may contribute to a learning signal that enforces morality. Several studies have focused on neural activity in response vicarious rewards in adolescence. In these studies, it was observed that adolescents showed ventral striatum activity when gaining rewards themselves, but also when their best friends gained rewards. Furthermore, this effect was larger for participants who reported higher friendship quality but was absent for unknown others (Braams et al. 2014). The same pattern of results – increased striatal activity for close others- was replicated by a study that focused on adolescents' family members. In adolescence, there is a well-established link between empathy, increased prosocial behavior and moral judgement (Eisenberg et al. 1995, 2005; Eisenberg-Berg & Mussen 1978).

Moral emotions in adulthood

A recent approach, mostly developed in adolescents and adults, has been to combine economic games (DG, UG, trust game), or new moral tasks (Rutledge et al. 2016; van Baar et al. 2019), with computational modelling and model-based fMRI to study the neurocomputational mechanisms underlying moral emotions. Using this approach, empathy, guilt and its anticipation, envy and other moral emotions, have been defined using computational models (Fehr & Schmidt 1999; Qu et al. 2022). These models formalize people's sensitivity to weigh personal benefits against the moral cost of violating internalized moral norms, such as harming others. Moral emotions emerge at the time of the decision when self/other interests are weighed (i.e. expected value) or at the time of outcome when (un)expected harms/benefits concerning self and others are revealed (i.e. experienced value). For example, empathy is associated with a higher rate of learning about actions that result in beneficial outcomes for other people as well as the neural drivers of prosocial learning in the subgenual anterior cingulate cortex (Lockwood et al. 2016).

Adults not only show inequity aversion to self-other distributions that disfavor them (i.e. disadvantageous inequity), they are also averse to unequal distributions that benefit them (i.e.

advantageous inequity) (Gao et al. 2018; Nihonsugi et al. 2015). Disadvantageous-inequity aversion has been linked to negative moral emotions such as envy (Blake et al. 2015; Fehr & Schmidt 1999), and engages the amygdala and posterior part of the insula (Feng et al. 2021; Gao et al. 2018). In contrast, when manipulating the social context in which the resource allocation occurs, advantageous inequity has been associated with social and mentalizing-related processes, involving the dlPFC, anterior insula and dorsomedial prefrontal cortex (Gao et al. 2018). This social context manipulation allowed researchers to dissociate the psychological and neural processes of payoff and inequity by modulating the salience of inequity but not the salience of absolute payoff. When causing pain to a coplayer (guilt context), adults cared more about advantageous inequity and became more tolerant of the disadvantageous inequity, compared with other conditions. Moreover, the dorsal anterior insula may modulate cognitive processes that generate expectancy for norm compliance, whereas ventral anterior insula could be linked to aversive emotions associated with inequality aversion that generate motivation for norm enforcement (Bellucci & Dreher 2020; Bellucci et al. 2018).

Guilt is closely related to inequity aversion because it both signals and constitutes the obligation of moral violators to balance the inequity created by their moral transgression (Gong et al. 2019). Guilt has been conceptualized as anticipation of a negative emotional state associated with the violation of personal moral rules, social standards or another's expectations (Chang et al. 2011). Recent models of guilt-aversion provide a precise quantification of the amount of guilt anticipated as the result of a given decision (Gong et al. 2019). According to these models, one's aversion to the possibility of experiencing future guilt prompts morally aligned decisions to minimize guilt anticipation. Guilt has been associated with activity in the ventral anterior cingulate cortex, posterior temporal regions and precuneus in adults (Bastin et al. 2016).

Shame has been associated with activity in the dlPFC, posterior cingulate cortex and sensorimotor cortex (Bastin et al. 2016). A difference between shame and guilt is that shame is a self-oriented emotion while guilt is other-oriented. This difference has important consequences on empathy for other people: while guilt tends to increase the empathic concern towards other people, empathic responses seem to be disrupted by the self-oriented distress associated with shame (Tangney et al. 2007). For example, the experience of guilt or inequity is strongly predictive of altruism (Gong et al. 2019; Hu et al. 2021a; Seara-Cardoso et al. 2016), suggesting that variability in the emotional impact of inequality on well-being can explain heterogeneity in altruistic behaviour (Rutledge et al. 2016). Similarly, adults are more likely to reverse ranks and reduce inequality when a social hierarchy is perceived as unfair (Foncelle et al. 2022). These findings indicate that moral emotions related to inequity aversion, guilt and shame guide individuals when making moral decisions weighing considerations between oneself and others and that moral emotions can be accounted mechanistically using a neurocomputational approach.

Moral emotions in older adulthood and ageing

By older adulthood, changes still occur in what may be considered moral emotions: empathy, guilt, pride, and inequity aversion. Of course, at the basic level ways moral emotions remain consistent. However, it is widely documented that older age is associated with higher levels of emotional well-being (Charles & Carstensen 2010) and lower rates of anxiety and major depressive disorder (Blazer 2003; Charles & Carstensen 2010; Fields et al. 2022), at least cross-sectionally. These increases in positivity occur despite decreased cognitive and physical capacity (Murman 2015). So how do our moral emotions change with senescence? When measuring emotional responses to inequity, older adults have been suggested to show greater aversion to inequity and an outcome bias that is insensitive to others' intentions (Margoni et al. 2021, 2023). In general older adults, aged 65+, are thought to rely more on outcomes than intentions (Margoni et al. 2021, 2023), consistent with a reduced use of theory of mind and model-based reasoning (**Figure 2**). This is despite possibly age-related differences in generosity, discussed later (Bailey et al. 2013; Cutler et al. 2021a; Mayr et al. 2024; Mayr & Freund 2020).

Studies also suggest that the emotional and affective aspects of empathy remain stable or increase in later adulthood (Beadle & de la Vega 2019; Beadle et al. 2012; Ze et al. 2014), although see (Chen et al. 2014). This is based on self-reported empathic responses to specific scenarios. Other work in an effort-based decision-making context has shown that both young (aged 18-35) and older (aged 60- 80) adults feel equally positive when they help another person, and these feelings of positivity drive cost-benefit analyses of their effortful helping (Lockwood et al. 2021).

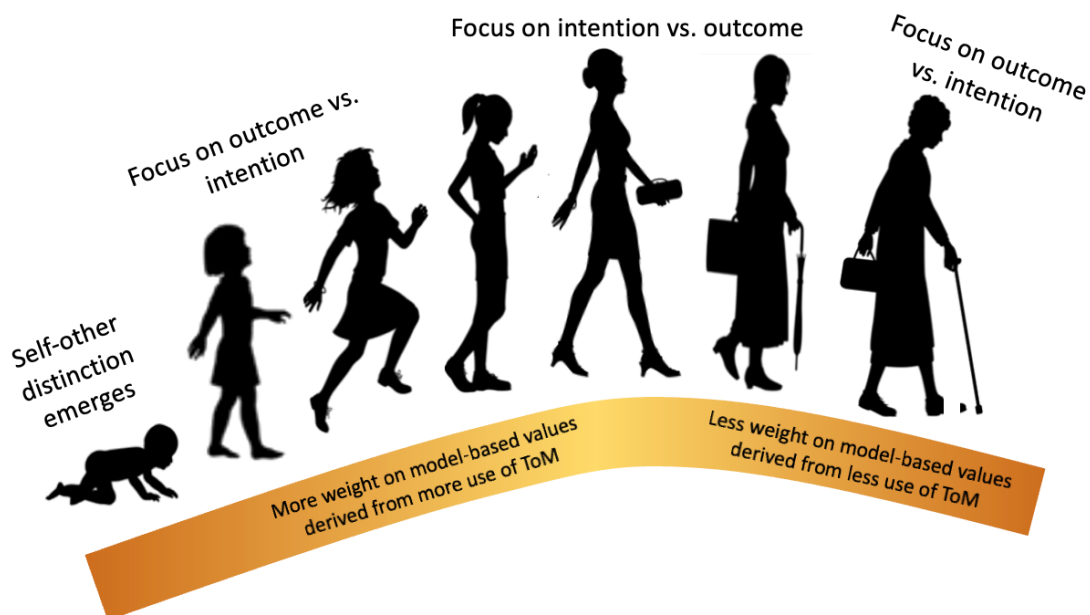


Figure 2. Moral learning and decision-making across the lifespan are underpinned by changes in the weight and influence of model-based values and the use of theory of mind (ToM). Self-other distinction emerges in infancy and supports the development of more complex moral emotions. A focus on the outcome vs. intentions of others' social decisions fluctuates from childhood to adulthood and old age and co-occurs with a different reliance on model-free and model-based learning. Model-based learning ability is highest in early to late adulthood and has a lower influence in childhood and older adulthood. In parallel, the use of theory of mind for moral decision-making increases from later childhood to adulthood before being used less in older age. These fluctuations in the reliance on model-based values and theory of mind could be critical for understanding moral learning and decision-making across the lifespan.

Learning and deciding about other's moral character

With the foundational architecture of moral emotions, the next step is to be able to learn and decide about the moral character of other people. Do we view others as behaving prosocially or antisocially? Are they trustworthy or not? Do we engage in punishment of those who have committed transgressions? Several experimental approaches have been developed to assess how we learn and decide about moral character, and these differ substantially from infancy to older adulthood. In infancy, most studies have used looking time experiments, and in adolescents and adults, complex economic games with multiple trials and computational models of behaviour have been deployed. Here we review how the ability to learn and decide about other's moral character differs from infancy to older adulthood within a value-based decision-making framework.

Learning and deciding about other's moral character in infancy and childhood

One crucial aspect of morality is the ability to reason about value-based decisions. In pre-verbal infants,

this can be measured using looking-time experiments where gaze at expected and unexpected events is taken as a proxy for reasoning about differences between them. Studies have compared preferences for actors that behave prosocially to antisocially and suggested that infants will attend more to a prosocial character (Hamlin et al. 2007; Ziv & Sommerville 2017). A systematic review of 27 experiments reported that 67% showed infants preferred a prosocial actor (Holvoet et al. 2016). This preference was present as early as 5 months. Failure to replicate these effects or demonstrate developmental differences in older infants may be due to definitions surrounding the social cues needed to capture prosocial behaviour. They may also be related to unique developmental trajectories and individual differences amongst infants. Moreover, looking time measures have also faced methodological challenges of being as unable to truly reveal infants' preferences (Tafreshi et al. 2014).

In childhood, when more complex methodologies can be used, studies show that from around age 6 moral character information influences children's evaluations of moral transgressions (Cameron et al. 2022), and children will engage in costly punishment to enforce fairness norms (McAuliffe et al. 2015). With co-occurring development in theory of mind and model-based reasoning (**Figure 2**) children's moral judgements become more intricate and incorporate notions of intent, causality and future repercussions (Cushman et al. 2013). This enables the development of more sophisticated forms of moral judgement in the transition to adolescence. Such changes support the ability to decide about others moral character, and eventually act upon these judgements when we decide to punish others in the case of third-party punishment (TPP) discussed in further detail in the following section, learning and deciding for others.

Learning and deciding about other's moral character in adolescence

As discussed previously, adolescents increasingly start to involve the intentions of others in their judgement of others moral behaviour, rather than focussing solely on the consequences or outcomes (Gummerum & Chu 2014; Güroğlu et al. 2009; van den Bos et al. 2011). However, the moral character of others is often not based on single events but instead may emerge over a series of interactions or observations. As such, judgement of moral character may rely on very basic learning mechanisms already present in infancy. Indeed, in the past decade several studies have provided evidence for the hypothesis that learning social values or learning in social context relies on basic value-based learning mechanisms that are already in place at an early age (Hofmans & van den Bos 2022; Lockwood & Klein-Flügge 2021).

As adolescents mature, there is a notable improvement in the capacity to optimally integrate recent outcomes into value estimates. Many studies also applied reinforcement learning models (**RL sidebar**) that have separate learning rates for positive and negative events, capturing sensitivities to rewards and punishments. Whereas initial studies suggested that younger adolescents may be more sensitive to negative outcomes and young adults put more weight on positive outcomes (Van den Bos et al. 2012), this pattern was not robustly replicated (Nussenbaum & Hartley 2019). Instead, the overall picture of developmental changes in learning rates suggests that the optimization of these rates may be fine-tuned to the specific learning context, and that it is this adaptive ability that increases with age. A study in a large sample of adolescents aged 9-18 (n=742) showed that in tasks where the absence of response is optimal for some stimuli, and therefore can be distinguished from reward learning, adolescents' learning from punishment improves with age, whereas learning rates from reward remain stable (Pauli et al. 2023). Finally, other studies that have focused on more complex tasks have shown that model-based contributions to learning increase across adolescence (Bolenz et al. 2017, 2019; Decker et al. 2016; Nussenbaum et al. 2020) which is modulated by increased cognitive abilities (Nussenbaum et al. 2020; Potter et al. 2017).

Most developmental studies on moral character have focused on learning whom to trust in an iterative version of the TG, where the participants play multiple rounds as the trustee with partners (real or fictive)

that differ in their level of trustworthiness. Consistent with previous studies on RL and social preferences, these studies have revealed that with age adolescents trust and trust evaluation of others becomes more pronounced (Fett et al. 2014; Sijtsma et al. 2023; van den Bos et al. 2012; Westhoff et al. 2020). Whilst there are very few changes in adapting to non-trustworthy partners there is an improvement in learning to trust a trustworthy partner (Sijtsma et al. 2023; Westhoff et al. 2020), most likely due to the decreasing sensitivity to rejection. Furthermore, Lee et al. showed that older adolescents are more likely to adapt their behaviour based on experience rather than the prior information they received about the moral quality of others (Lee et al. 2016). Therefore, older adolescents become better at updating the model they have of the other player. Finally, Fett et al., (2014) also indicated that these changes were paralleled by increased brain activation in regions linked to social and self-regulation, such as the TPJ, posterior cingulate and the precuneus. The activation of these networks further supports the idea that with age the learning processes may become more model-based (**Figure 2**) and that adolescents spend more time forming and updating a model of the other player.

Moral learning and decision making about others moral character in adulthood

Moral choices about others

By adulthood, people make complex trade-offs between self and other harm and studies have examined the neural mechanisms underlying these computations. For example, when people trade off self-monetary gains/losses against moral costs/benefits concerning others (Qu et al. 2019, 2020) or when they weigh pain to themselves and others (Crockett et al. 2015, 2017). In these paradigms, the notions of moral cost and harm aversion are important to explain trade-offs between moral and monetary values (Crockett et al. 2017; Qu et al. 2019, 2020). These computations reflect specific features of the choice options (e.g. amount of money donated to a bad cause and to oneself, or, the difference in the quantity of money and number of electric shocks) to their underlying decision values.

When making choices that weigh moral against monetary cost/benefit, areas of the brain involved in valuation are engaged (Qu et al. 2022). In one study, a trade-off between moral cost and self-monetary benefit engaged the lateral PFC and the anterior insula (Qu et al. 2019). In contrast, a decision value signal encoding the difference between self-monetary cost and compliance with one's moral values (i.e. moral benefit) engaged the ventral putamen. This is consistent with distinct brain systems for treating violations of moral norms as aversive outcomes on one hand, and another system treating compliance with moral rules as a rewarding outcome. The right TPJ, dIPFC, anterior insula have also been reported to be engaged in encoding moral values (Ugazio et al. 2019). In particular, the lateral PFC responds more strongly when harming others for a small relative to a larger profit (Crockett et al. 2017), to moral norm violations (Chang & Koban 2013; Ruff et al. 2013) and computes variables of moral utility (Bellucci et al. 2019; Sai et al. 2021; Speer et al. 2020) or weighs differences between honesty and self-interest (Dogan et al. 2016; Greene & Paxton 2009; Zhu et al. 2014).

The neural bases of another type of dishonest behavior, corruption behavior, has also been investigated (Hu et al., 2021; 2022). When a power-holder decides to accept or reject a bribe, they consider two types of moral cost brought by taking bribes: the cost of conniving with a fraudulent briber, encoded in the anterior insula, and the harm brought to a third party, represented in the rTPJ. These moral costs were integrated in the vmPFC and the dIPFC was selectively engaged to guide anti-corrupt behaviors when a third party would be harmed. Understanding the neurocomputations engaged in moral tradeoffs in adults is not only useful at a mechanistic and fundamental level, AI-based anticorruption tools may also benefit from these recent computational models (Köbis et al. 2022).

Moral learning about others in adults

Three types of moral learning phenomenon have been described at the neurocomputational level in adults when learning a new set of moral rules, when learning the moral character of strangers, and when learning the moral character of others (Qu et al. 2022). First, when learning a new set of moral rules/norms, a RL model showed that a PE is encoded in brain regions engaged in moral choices, including the vmPFC/mOFC, the anterior insula and the striatum. The ability to learn moral norms, such as criminal laws and religious commandments has also been investigated (Cushman et al. 2017; Siegel et al. 2018, 2019). Second, when learning the moral character of strangers through observation of their actions, a few studies in adults have identified a brain system including the rTPJ and caudate nucleus. This network responds with variables evolving with the impression of agents' moral character and according to the way they shape subsequent moral judgments (Bellucci et al. 2019; Fouragnan et al. 2013). The rTPJ is associated with a PE signal updating the impressions of others' morality (Park et al. 2020) while caudate nucleus activity has been associated with updating others' trustworthiness (Fouragnan et al. 2013). Third, learning about the moral characters of others has also been explained by an asymmetric Bayesian updating mechanism in which beliefs about the morality of bad agents are more uncertain than beliefs about the morality of good agents (Siegel et al. 2018, 2019). Together, these studies indicate that different forms of learning processes can be formalized by different types of PE: norm PE, PE about harmful outcomes occurring to others, and PE by observation of other's moral actions.

Learning and deciding about moral character in ageing

Studies on judgement and decision-making in older adults have suggested that there are age-related shifts in affective processing and deliberative judgment, that may be key to understanding differences in moral judgment. As mentioned previously, positivity biases may increase in age and the influence of executive functioning and theory of mind may reduce due to age-related decline. These shifting lifespan patterns could underpin differences between young and older adults in moral judgements, although paradigms such as the harm aversion paradigm used in young adults (Contreras-Huerta et al. 2020; Crockett et al. 2015) are yet to be used in older samples. Using simple tasks of moral judgment, one study reported that older participants relied less on intentions and more on outcomes compared to younger participants (Margoni et al. 2018), reminiscent of earlier developmental differences. Intriguingly, these age-related differences were associated with a decline in older adults' theory of mind abilities (Figure 2). Indeed, there is debate as to whether this outcome-to-intention shift seen in children and older adults is reflective of a fundamental conceptual change (Cushman et al. 2013) an improvement in theory of mind abilities and model-based reasoning (Margoni et al. 2018).

A longitudinal study additionally showed that while moral reasoning skills generally improve through the lifespan they start to reduce in old adulthood (Armon & Dawson 1997). Moran et al. (2013) proposed that ageing differences in moral judgment are related to theory of mind impairments but also discussed the possibility that they may also be related to a more general cognitive decline (Moran 2013). Future studies that take a model-based approach to capture theory of mind could be crucial here. They contain parameters such as the beta parameter that can capture noisiness in decision-making and inattention (Lockwood & Klein-Flügge 2021; Zhang et al. 2019). By using a computational framework, differences in theory of mind ability and general decision-making ability could be separated.

Moral learning and deciding for others

In addition to learning about moral character, sometimes we simply make decisions that have an impact on another person and therefore have moral responsibility. Examples include when we learn to help and avoid harming others, or when we learn and decide to punish other people. These decisions are governed by normative principles to help and not harm. Such social decisions can often have more wide-reaching moral implications for society. For example, a commons dilemma where my decision to fly to Ibiza for a winter break directly benefits myself but can negatively impact others and future

generations. In addition, in order to be prosocial, we need to understand others' preferences to know to help them, an ability likely to be influenced by theory of mind. So how do we learn and decide when we must do so on behalf of another person?

Learning and deciding for others in infancy and childhood

Studies on learning and deciding for others in infancy are somewhat limited, given the challenges of measuring learning and decision-making in this age group, and that it is a developmental stage with a strong self focus as described above. However, capacity for associative and reinforcement learning (**RL Sidebar**) in non-moral settings does emerge early in life. Ten-week-old infants increase the rate at which they kick their feet toward a brightly coloured wooden mobile compared to a mobile that does not provide reinforcement (Rovee & Rovee 1969). Six-month-old infants can learn to look more often at a coloured shape if it leads to a video cartoon (reward) than if it leads to nothing (Tummeltshammer et al. 2014). This early propensity for associative learning is clearly foundational in moral development.

Whilst some researchers have suggested that learning and deciding to help others is highly prevalent in our early years (Beier et al. 2014; Hamlin 2013) others have challenged whether observations of toddlers helping behaviours are evidence of altruism and cooperation, or simply reflect an interest in what others are doing and infants wanting to participate in adult activities (reviewed in (Carpendale et al. 2015)). In one of the first studies to report that toddlers learn and decide for others, (Rheingold 1982) reported that toddlers would help with household chores and would do so unprompted, suggesting that deciding for others occurs early in development. 18 months may decide to help others even if it is effortful, and by age 20 months they will stop playing with toys to help an experimenter (Warneken & Tomasello 2009). These researchers interpreted such behaviour as reflecting evolved altruistic tendencies.

In general, older children ages 3 to 6 decide to help both adults and peers in need, and this interpretation has received less controversy (Paulus 2020). By age 8 aspects of theory of mind and model-based reasoning have developed (**Figure 2**) as evidenced by the observation that children will reduce their own resources to make sure rewards are shared equally with a partner (Lee & Setoh 2023). It is important to note that in economic games developmental changes could reflect a reduced valuation of rewards for oneself, rather than a higher prosocial preference to benefit others as the cost is financial. The valuation of reward is crucial to understand across all life stages including older adulthood where older adults have accumulated more wealth, which we will return to later.

Another way in which we learn and decide for others is when we engage in third party punishment (TPP). A typical TPP paradigm involves three parties: a perpetrator, a victim, and a third party who observes an interaction between the first two. The perpetrator is given the opportunity to harm the victim — often through the allocation of resources — in a way that violates a social norm or rule. The third party observes this interaction and is then given the chance to punish the perpetrator, or help the victim, usually at some cost to themselves (Fehr & Fischbacher 2004a). Empirical evidence supports that TPP is central to constructing morality. Young children expect third-party punishment to occur to perpetrators that harm ingroup members (Decety & Cowell 2018). Later, an understanding that harmful actions cause suffering emerges, followed by the integration of rules dependent on social contexts and cultures (Decety & Cowell 2018). These processes may be underpinned by the maturation of frontal lobes such as the vmPFC where age-related increases in activity in response to viewing scenarios depicting intentional vs. accidental harm occur from age 4-37 (Decety et al. 2012).

Learning and deciding for others in adolescence

Taking an early lifespan perspective, Piaget (Piaget 2013) proposed that development of distributive justice, fair resource distribution, goes through distinct developmental phases; 1) young children view

fairness egocentrically, with a focus on self-interest, 2) around 7-8 years they see justice as obedience to unchangeable rules, 3) when they approach adolescence they recognize rules as social constructs open to interpretation, and 4) older adolescents appreciate that true equity may require different treatment for different people to address individual needs and circumstances. However, more recent studies, found that young children aged 3 to 8 years already distinguished among various situational and personal factors, such as merit (Baumard et al. 2012; Kanngiesser & Warneken 2012), and need (Li et al. 2014; Paulus 2016). Although young children begin to distinguish various factors that influence fair distribution, studies also report that more complex coordination processes emerge in adolescence (Almås et al. 2010; Kienbaum & Wilkening 2009).

As in infancy, one behavioural measure to gauge responses to the fairness of distributions is TPP. A developmental study of TPP by Gummerum and Chu (2014) showed that children and adolescents consistently punished players who proposed unfair offers in a DG/UG, however both age groups focused mainly on outcomes rather than intentions. However, in a second study (Gummerum et al. 2020) showed that adolescents' punishment became more proportional to the inequality inflicted by the perpetrator with age. In a similar set of studies, participants observe the exclusion of an individual in the virtual ball-tossing game (Cyberball), and can punish the perpetrator or help the victim by dividing money between themselves, the perpetrators, and the victim. One study demonstrated a gradual age-related increase in money given to the victim from age 9 to 22 and a gradual decrease in money allocated to the excluders from age 9 to 16 (Will et al. 2013). Importantly, this study also showed that perspective-taking predicted both compensation of the victim and punishment of the excluders. In a developmental fMRI study, it was found that observing exclusion activated regions linked with in mentalizing (i.e., mPFC), particularly among highly empathic adolescents. Additionally, adolescents who displayed more activity in these regions during observed exclusion subsequently showed more prosocial behaviour towards victims. In line with these findings, Tousignant et al ((Tousignant et al. 2018)) showed that adolescents who were more empathic and prosocial had more activation in the TPJ and mPFC. Taken together, these studies suggest that deciding about others also increasingly involves the integration of more complex situational factors as well as theory of mind.

The TPP studies show that adolescents are not passive bystanders but are willing to take moral responsibility and situational factors into account. However, to be able to support others in more dynamic situations it may be necessary to put in more effort and to learn how to best do this or learn about their preferences. The prosocial learning task captures how we learn to help others (Lockwood et al. 2016). A recent study with adolescents examined performance differences in a prosocial and self-benefitting learning task where outcomes were for self or others. It was found that performance in the learning task improved with age. Moreover, age-related improvement in performance was larger when learning for others than when learning for self. Computational modeling showed that improved performance was associated with lower learning rates in older adolescents, which indicates that they take a longer history of choices into account. At the neural level, increased performance was paralleled by an age-related increase in vmPFC activity when learning to reward others (encoding a prosocial PE) (Westhoff et al. 2021). Activity in vmPFC was also correlated with measures of perspective taking, suggesting that this processes further supports learning how to help others. In line with these results Kwak and others found that children/adolescents, compared to adults, were more sensitive to rewards directed to a charity than to self (Kwak & Huettel 2016), suggesting that these results extend to society at large.

Learning and deciding for others in adulthood

In adulthood, studies have also used similar paradigms to those used in adolescence to examine how we learn about outcomes for others. Prosocial learning based on moral concerns such as learning to avoid electric shocks for another person (Lockwood et al. 2020b) or when learning to choose between options paired with probabilistic monetary rewards for oneself and shocks for a confederate has been

studied (Fornari et al. 2023). When learning to avoid harm to others versus self, a stronger relative balance was observed toward model-free over model-based learning. The caudate nucleus distinguished PE for avoiding harm to others versus self (Lockwood et al. 2020b). Ventral striatum encoded PE of pain avoidance for self and others and the subgenual anterior cingulate cortex (sgACC), a region known to be implicated in moral agency (Zahn et al. 2020), was engaged when deciding to stay vs. switch after no pain for others vs self. The sgACC is also engaged in prosocial PE (i.e gaining rewards for others) (Lockwood et al. 2016, 2018) and in receiving unexpected positive feedback from others (Will et al. 2017).

More complex decisions for others come in the form of TPP which has been investigated by combining the UG with fMRI. Participants, as observers, may pay to punish unfair allocations of endowments by one of two others. fMRI meta-analyses of social punishment have reported common (dlPFC and bilateral AI) and specific brain regions (AI) for second- and third-party punishments (TPJ) (Bellucci et al. 2020; Feng et al. 2015). Moreover, inequity aversion has been proposed to be a key motive driving TPP (Blake et al. 2015; Fehr & Fischbacher 2004b; Raihani & McAuliffe 2012), with payoff difference between proposer and receiver defining the extent of inequity (Zhong et al. 2016). Some brain regions representing TPP are similar to those representing inequity aversion, including the ACC and AI (Zhong et al. 2016). Engagement of these regions is positively associated with the detection of distributional inequity, while dlPFC activity is associated with the assessment of intentionality to the norm violator.

One important limitation of these TPP studies is that they have ignored the possible social ties between the third-party and the dictator, simply assuming that they were strangers. A recent study showed that third-party punished norm violators more severely as social distance between them increased, and disentangled key computations contributing to TPP, such as inequity aversion, social distance between participant and norm violator and integration of the cost to punish with these signals (Tang et al. 2023). The inequity aversion and social distance brain signals and the cost to punish were integrated in a value signal of sanctions that modulated activity in the vmPFC. This study reveals the neurocomputational underpinnings of TPP and how social distance modulates the enforcement of moral norms in humans.

Pushing further the importance of social relationships between a wrongdoer and the recipient of an immoral action, it has been shown that immoral behaviours vary depending on who receives specific benefits (Earp et al. 2021; Qu et al. 2020). To identify the neurocomputational mechanisms underlying such moral flexibility, adults were presented with offers requiring a tradeoff between a moral cost and a benefit for either oneself or a charity (Qu et al. 2020). Participants were more willing to obtain ill-gotten profits for themselves than for a charity, driven by a devaluation of the moral cost when deciding for their own interests. Subjective valuation of the immoral offer recruited the vmPFC regardless of beneficiaries. Individual differences in moral preference modulated choice-specific signals in the dlPFC according to who benefited from the decisions. These findings provide insights for understanding the neurobiological basis of moral flexibility.

Together, these neuroimaging studies in adults indicate that moral concerns may act in concert with inequity aversion and the willingness to punish norm violators, even when one is not directly involved as a victim of the norm violation.

Learning and deciding for others in ageing

Although human aging is often associated with declines in cognitive and behavioural processes including memory, learning and motor abilities, how moral decision-making differs as we get older is less well studied. Intriguingly, recent research suggests that people believe that morality declines in older-age (Mastroianni & Gilbert 2023), but in fact, several studies suggest that moral learning and decision-making for others may be preserved or even enhanced in older age (Cutler et al. 2021a,b; Hubbard et al. 2016; Kettner & Waichman 2016; Mayr & Freund 2020). One challenge with

understanding moral learning and decision-making in this age group is that most of the literature has used economic games. Such games may be unable to distinguish whether lifespan differences reflect differences in valuing rewards or distinctly moral and prosocial behaviours (See Future Issues).

Older adults (age 60–80) have been shown to have preserved prosocial learning, despite a decline in learning that benefits only themselves (Cutler et al. 2021b). This prosocial learning for others in older adults also varies with subclinical psychopathic traits including empathy and guilt such that those older adults highest in psychopathic traits learn slowest to help the other person. In this study reinforcement learning was model-free and it would be interesting for future studies to examine whether such prosocial learning is preserved in a model-based context, where older adults have been suggested to have greater learning challenges (Eppinger & Bruckner 2015a; Hämmerer et al. 2019).

When examining basic economic games such as the dictator game studies have suggested an increased preference to be generous towards others with advancing age (Engel 2011) a result replicated around the world (Cutler et al. 2021a). However, the bias to help people perceived as in one's in-group rather than out-group also inflates (from age 18-99) (Cutler et al. 2021a). This in-group bias is robust even in very young children (Over et al. 2018). It would be interesting for future studies to compare in-group bias across the whole lifespan to examine non-linear impacts on learning and deciding for others. Intriguingly, studies of differences in TPP in older compared to younger adults are not available, to the best of our knowledge, an important avenue for future research.

Moral influence and contagion

Finally, moral learning and decision-making can also be under the influence of other people including peers, strangers, or society. Several studies have suggested that humans are susceptible to such moral influence and the extent to which they are may differ from infancy to old age. In a historical period of huge social information available online, it is essential to understand how such susceptibility differs across the lifespan, and whether certain life stages are associated with specific vulnerabilities to moral influence by others.

Moral influence and contagion in infancy and childhood

Evaluating whether infants and children are morally influenced by others is challenging experimentally. However, theoretically, early models of development highlight how observational social learning occurs the context of aggression (Bandura 1965). Others have emphasised associative learning between actions and outcomes is a key mechanism for developing moral architecture (Heyes 2012).

Observational learning is a fundamental ability apparent from the first years of life (Foti et al. 2018; Herold & Akhtar 2008; Matheson et al. 2013). If adults show their intention prior to demonstration, 16-months-old infants can learn tool use by observation (Fagard et al. 2016). But are they influenced by learning about moral behaviours? One study suggested 5-7 year olds who observed someone sharing were more likely to share themselves. Ma et al (2018) found that children aged 5 were more honest after observing a classmate benefit from being honest (Ma et al. 2018). Together these results suggest that the basic mechanisms of action-outcome pairing and moral influence emerge from infancy to childhood. In later years these abilities become more sophisticated.

Moral influence and contagion in adolescence

Adolescence is a period of strong changes in socially motivated behavior and it may therefore not be a surprise that adolescents tend to respond more strongly to information from others, specifically their peers, compared to other age groups (Albert et al. 2013; Blakemore & Mills 2014; Molleman et al. 2019, 2022; Silva et al. 2016). Whether this increased peer influence is negative or positive appears to be

context-dependent. Social influence among adolescents is often associated with increased risk taking and negative outcomes (e.g. anti-social behavior and substance abuse (Chein et al. 2011; Ciranka & van den Bos 2019; Dishion & Tipsord 2011; Reyna & Farley 2006). Indeed, in many experimental settings risky behavior of peers can lead to increased risky behavior (Chein et al. 2011; Gardner & Steinberg 2005; Smith et al. 2014), but several studies also showed that observing risk-averse peers or risk-averse advice had at least the same amount of impact on reducing risky-behavior (Bingham et al. 2016). Similarly, observing prosocial behavior of peer can also both in- and decrease prosocial behavior of adolescents (Sullivan et al. 2022; van Hoorn et al. 2016).

Recently, the effects of peers in different domains have been studied, which suggested that there is 1) a single factor underlying the developmental changes in social information use in adolescence, and 2) a significant reduction in sensitivity to social information during this period. Pinho et al., have shown that adolescents are influenced by observing strong disapproval of risk-taking or strong approval of prosocial behaviour (Pinho et al. 2021) and this may be linked to TPJ. For example, variability in TPJ response in adolescents has been related to their own charitable giving (Tashjian et al. 2018). Thus, information about norms and or observations of single individuals can change adolescents' attitudes and behaviours. Researchers have also developed paradigms where participants receive positive (i.e., acceptance) or negative (i.e., rejection) feedback from peers (Achterberg et al. 2018; Guyer et al. 2012; van Hoorn et al. 2016). In one imaging study adolescents gave more, at their own expense, when they were being observed, and even more when they received feedback (Van Hoorn et al. 2016). Importantly, peer presence was associated with activation in the mPFC, TPJ, precuneus, and STS, and adolescents' TPJ activity was associated with their level of generosity.

In sum, this pattern of results is consistent with a shift from model-free to more model-based reinforcement learning (**Figure 2**) which is associated with increased engagement of brain regions such as the TPJ.

Moral influence and contagion in adulthood

In adults, social influence has been proposed as an important mechanism to explain why people follow others' choices (Lee & Chung 2022; Toelch & Dolan 2015; Yu et al. 2021). In a moral context, both the size of a jury judging a crime scenario and the confidence that each jury member has in their own moral judgment determine how much a given individual adapts to the judgment of the jury (social influence) (Park et al. 2017). At the time of judgment adaptation following influence from others, individuals trade off the credibility inferred from their own confidence levels against the credibility of social information. The dACC represents belief updates during moral judgments when conforming to other jurors, while the lateral frontopolar cortex monitors the changes in credibility assigned to social information. These results provide a neurocomputational understanding of social influence on moral choices.

Social influences can also affect how we consider our moral choices in the eyes of others. Indeed, we tend to behave in a more egoistic manner under guaranteed anonymity and more pro-socially when observed by others (Izuma 2012). The influence of being observed by others has been investigated when making both moral and amoral choices (Obeso et al. 2018; Qu et al. 2020). Two types of choices were considered: whether to earn money by contributing to a 'bad cause' and whether to sacrifice money to contribute to a 'good cause'. Adults were more likely to choose the prosocial option when they had to make a public donation. Regardless of the type of dilemma, the ACC, AI and the rTPJ were more engaged in public than in private settings. Moreover, distinct valuation systems were engaged to solve these dilemmas: AI and IPFC when weighing monetary benefits and moral costs, and ventral putamen when weighing monetary costs against compliance with one's moral values.

When observing dishonest individuals, adults, like infants, might progressively become more and more dishonest (Dimant 2019; Gino et al. 2009). Thus, learning about others' behaviour can dynamically

change one's own preferences or bias one's own valuation process (Lee & Chung 2022; Yu et al. 2018). The dlPFC may integrate social factors such as moral norms as well as moral preferences into the decision process during moral choices (Buckholtz 2015; Carlson & Crockett 2018; Crockett et al. 2017). One study in adults showed that the extent to which participants engage in self-serving dishonesty increases with repetition and this effect is associated with a reduced amygdala sensitivity to the history of dishonest behavior (Garrett et al. 2016). Together, these studies suggest social influence continues to be a strong driver of following moral norms in adulthood.

Moral influence and contagion in ageing

Like adolescents, older adults show an increased or preserved processing of rewards in social contexts, and this pattern is even present across species (Almeling et al. 2016; Foulkes & Blakemore 2016; Samanez-Larkin & Knutson 2015). Processing rewarding outcomes is a fundamental mechanism that is the first stage of moral influence and contagion, and as already discussed, is apparent in childhood. Recent evidence suggests in non-moral contexts that older adults might be more affected by social conformity of economic preferences (Su et al. 2024) particularly when these preferences are impulsive compared to patient. Experience sampling work suggests that for daily desires, self-control increases from young to older adulthood and social influence decreases (Castrellon et al. 2023).

These differences in susceptibility to social and moral influence may again reflect differing reliance on theory of mind and model-based strategies (**Figure 2**). It is possible that resisting moral pressure depends on theory of mind to reveal the intention of others which could be learnt by observation. Several studies have suggested that theory of mind ability, as measured by tasks where participants infer others' mental states by viewing faces, cartoons, or stories - is typically impaired in older adults (Kemp et al. 2012), **Figure 2**). Importantly, such impairments are at least partly independent of general cognitive decline (Kemp et al. 2012). One study reported age-related improvements in theory of mind in a vignettes task (Happé et al. 1998), yet a later meta-analysis supported older adults performing more poorly than younger adults across all theory of mind measures (Henry et al. 2013). Future studies incorporating the need to engage in mentalising during actual social interactions, and in a value-based framework (e.g. (Hampton et al. 2008; Hill et al. 2017) are needed to precisely measure index theory of mind ability in older adults. In terms of neural correlates, several studies have suggested that connectivity between frontal and parietal areas, often suggested to support theory of mind (Koster-Hale & Saxe 2013; Lockwood et al. 2020a; Wittmann et al. 2018), changes in older adulthood (Setton et al. 2022). Such changes may underpin these cognitive and affective differences.

Summary

We reviewed four key concepts that may be fundamental for understanding moral learning and decision-making across the lifespan (**Figure 1**). These were learning and experiencing moral emotions, learning and deciding about moral character, learning and deciding for others, and moral influence and contagion. These concepts show key similarities and differences across the lifespan from infancy to older age. In the earliest years, a sense of self-other distinction is foundational for the development of many key abilities. Sensitivity to the intention vs. the outcome of decisions is also crucial for moral judgement and learning and deciding for others which differs with age, interestingly being the most similar in our earliest and oldest years. Third-party punishment may develop early in life, yet we still know little about how these processes may differ during senescence. Across all ages, basic shifts in the influence of theory of mind and the balance between model-free and model-based reasoning appear important to support aspects of morality (**Figure 2**). As well as these general conclusions, future challenges and opportunities remain.

Future issues

Domain-general and domain-specific moral learning and decision-making

It remains unclear whether the learning processes involved in moral cognition engage distinct algorithms and different neural implementations from non-moral learning (Hopp et al. 2023; Lockwood et al. 2020a; Qu et al. 2022). Some advocate social learning can be explained by domain-general learning processes at the algorithmic level (Heyes 2012, 2018; Heyes & Pearce 2015; Lind et al. 2019), while others argue that it requires metacognitive knowledge about whom to learn from (Heyes 2016; Kendal et al. 2018). At the implementational level, there are arguments for common or distinct neural processes involved in social and moral vs. non-social learning (Lockwood et al. 2020a; Vogel & Lockwood 2024). The paradigms used are crucial here. Many older adults have accumulated more wealth than younger adults, and therefore economic games that have a purely financial cost may hide developmental differences. Instead, it is possible to use other costs to oneself, such as time and effort, or calibrate reward values across ages. For example, in younger children, a choice can be given between a financial reward and an object of equal value.

The importance of longitudinal studies

Most studies reported in this review present cross-sectional data, and often compare one or two age groups that represent a small slice of the whole lifespan. This lack of longitudinal studies may not account for shifts in social norms and thus cohort effects (Baltes 2009). Longitudinal studies would require the consistent use of the same task for participants of all ages. Thus far, versions of economic games have been useful given their simplicity and game like nature. New advances in designing paradigms based on theories in ecology could also be beneficial given that these probe cognitive processes that the brain evolved to solve (Gabay & Apps 2021; Scholl & Klein-Flügge 2018). Computational modeling using a consistent formalization of learning and decision-making processes can further harmonize the results of moral behavior in different age groups and can provide deeper insights in the developmental processes that lead to changes in behavior with age (van den Bos et al. 2018). In developmental computational neuroscience, researchers have mainly focused on the developmental changes in certain parameters. However, it is also possible that it is not only the parameters of a model that changes with age, but rather there is a shift in strategies, or moral heuristics (Gigerenzer 2008; Lindström et al. 2018; Sunstein 2003), thus different models that describe the behaviour best for different age groups (van den Bos et al. 2018). Finally, it is important that if variables of computational models are being used to compare age groups these are robust and reliable (Schaff et al. 2023; Waltmann et al. 2022), here hierarchical Bayesian modeling can help, specifically if there are only a few data points per individual to model.

Atypical moral development across the lifespan

When examining lifespan differences in moral learning and decision-making most of the research has focussed on typical rather than atypical development, since studies of atypical development often compare groups of individuals rather than differences across age. However, important insights can be gained by understanding the trajectories of atypical development (Hu et al. 2021). For example, conduct disorder, which may be considered the archetypal moral disorder is associated with behaviours which violate the rights of others and an absence of certain moral emotions such as empathy and guilt (Blair 2013; Fairchild et al. 2019; Frick & Kemp 2021; Pauli & Lockwood 2023). In addition, in a study with the mini-UG adolescent delinquents showed they cared less about the intentions behind unfair offers, and this behaviour was associated with reduced activation in the TPJ (van den Bos et al. 2014). Importantly conduct problems often onset either in childhood or adolescence and there is little evidence that it occurs later in life. Indeed, cross-sectional studies have shown that psychopathic traits are lower in older compared to younger adults (Cutler et al. 2021b). Studies that follow atypical development longitudinally are crucial as well as more carefully documenting the typical trajectories over longer time

scales to understand the mechanisms behind possible reduced levels of psychopathy and antisocial behaviour in later life.

Artificial Intelligence and lifespan development

One interesting implication of the recent development of computational models of moral choices across the lifespan is to consider how future artificial agents (e.g. automatic cars, robots, bots.) will be able to flexibly adapt to moral behavior of people from different ages (from children to older adults) (Bonneton et al. 2024; Köbis et al. 2022). For example, recent computational models of theory of mind in children indicate that the same computational model of theory of mind cannot be applied to children between 3-8 and above 8 years old (Nong et al. 2023; Philippe et al. 2022). It may therefore become necessary to equip artificial agents not only with algorithms mimicking computations used for moral choices from the adult human brain (Philippe et al. 2022), but also with algorithms accounting for computations accounting for moral choices of young children or older adults.

[Sidebar] Reinforcement Learning

Reinforcement Learning (RL) describes how an agent learns to make optimal decisions in an environment. Q -Learning is a Model-Free RL (MF-RL) algorithm that seeks to find the best action (a) given the current state (s) (Watkins & Dayan 1992). During learning the Q -value, a "quality" score for a state-action combination, is updated by comparing the experienced outcome (r) with the expected outcome ($Q(s,a)$). The extent to which the Q -value is updated is regulated by the learning rate (α):

$$Q_{t+1}(s,a) \leftarrow Q_t(s,a) + \alpha[r_t - Q_t(s,a)]$$

Model-Based RL (MB-RL) involves the agent creating a model of its environment and using this model to plan actions by simulating future steps (Dayan & Berridge 2014). This allows the agent to anticipate the consequences of actions without needing to try them all. However, building a model takes up more cognitive resources than MF-RL. Developmental studies have shown asymmetries in learning rates for outcomes that are better or worse than expected (Van den Bos et al. 2012), and a shift from MF-RL towards more MB-RL in adulthood (Decker et al. 2016), with a later reversal to MF-RL in ageing (Eppinger & Bruckner 2015b). RL models can also explain how a history of pairing social phenomena with positive or negative outcomes influences complex moral behaviours (Christopoulos et al. 2017; FeldmanHall & Dunsmoor 2019).

Definitions

In group bias is the tendency to favour those who are perceived as belonging to one's own group over other groups.

Inequity aversion concerns decisions that minimize inequity in outcomes, as the difference between one's own material self-interest and others' payoffs.

Vicarious rewards: Rewards received by others.

Empathy is the capacity to understand and vicariously experience the affect of other people.

Theory of mind also known as mentalising is the ability to attribute mental states such as beliefs, desires, and intentions to other individuals.

Intention a mental state in which the agent commits themselves to a course of action.

Third-party punishment is when individuals punish transgressors or norm violators who have not harmed them directly.

Guilt occurs when the violation of social norms induces harm or suffering to other individuals, typically in a relationship or among members of the same group.

Shame is a 'self-focused negative emotion' experienced when a person believes that she transgresses certain rules. Shame is related to how we perceive ourselves.

Envy refers to a comparison between someone's negative situation and another individual's positive situation.

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